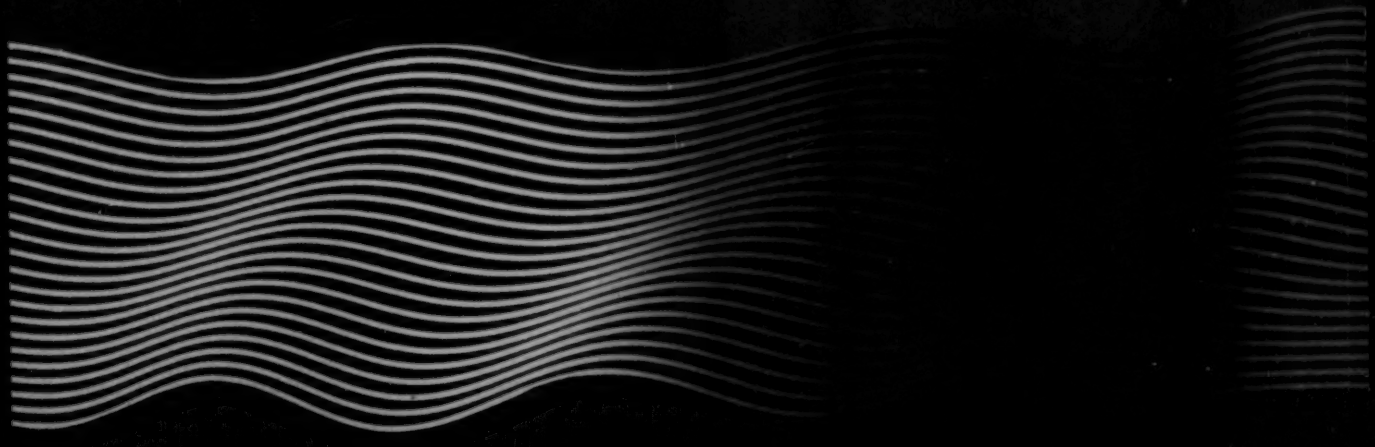
National Research Council Canada

Conseil national de recherches Canada

NRC · CNRC

Canadian Journal of Fisheries and Aquatic Sciences

Journal canadien des sciences halieutiques et aquatiques



ISSN 0706-652X / CJFSDX 54(Suppl. 1) 1–235 (1997)

The *Canadian Journal of Fisheries and Aquatic Sciences*, previously published as *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, and *Journal of the Fisheries Research Board of Canada* 1938–1979, is issued monthly to form annual volumes of 12 numbers plus supplements.

Editorial policy: The *Journal* publishes original research articles, critical reviews, perspectives (essays of opinion or hypothesis), and comments. Papers may concern cells, organisms, populations, ecosystems, or processes that affect aquatic production systems, and they should lead to identifiable conclusions or synthesis, which variously may amplify, modify, question, or redirect accumulated knowledge embodied in contemporary perceptions of a particular state of fisheries and aquatic sciences. They should demonstrate clearly a contribution to knowledge beyond the confirmation state. Originality should relate to more than the particular (a certain year, place, taxon, or chemical compound) such that existing understanding is reformulated or extended.

Manuscripts for publication should be submitted to **Dr. D.G. Cook**, Canadian Journal of Fisheries and Aquatic Sciences, NRC Research Press, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada (613-993-2209; fax: 613-952-7656; e-mail: journal.cjfas@nrc.ca).

Submissions in either English or French are acceptable. The information must be original, that is, not copyrighted, published, or submitted elsewhere except in abstract form or unless by written consent of the Editor. NRC accepts no responsibility for statements or opinions expressed by a contributor. Acceptance of an advertisement, announcement, or other material does no imply endorsement by either the *Journal*'s Editors or NRC. The use of proprietary names does not imply endorsement of the product or company.

Correspondence concerning accepted manuscripts and corrected proofs should be sent to NRC Research Press, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

Instructions to Authors are published once a year in the first issue of each volume. Copies are available from NRC Research Press or from our Web site. The **Publication Policy** of NRC Research Press is also available at our Web site:
http://www.nrc.ca/cisti/journals/rj.html

Microfilm: Issues from 1934 through the current volume can be purchased on 16- or 35-mm microfilm. Photocopies of individual articles or issues can be purchased from University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, U.S.A.

U.S. periodical postage paid at Champlain, N.Y., and at additional mailing offices. Attention U.S. POSTMASTER: Send address changes to **Canadian Journal of Fisheries and Aquatic Sciences**, c/o USACAN Media Distribution Center, P.O. Box 2888, Plattsburg, NY 12901, U.S.A.

Publié sans interruption depuis 1901, le *Journal canadien des sciences halieutiques et aquatiques* a paru sous plusieurs titres : *Contributions to Canadian Biology* 1901–1925, *Contributions to Canadian Biology and Fisheries* 1926–1934, *Journal of the Biological Board of Canada* 1934–1937, et *Journal of the Fisheries Research Board of Canada* 1938–1979. Le *Journal* paraît tous les mois, formant ainsi un volume de 12 numéros, et offre en plus jusqu'à deux suppléments par année.

Politique de rédaction : Le journal publie des articles fondés sur une recherche originale, des critiques, des essais portant sur une opinion ou une hypothèse (perspectives) et des commentaires. Les textes peuvent avoir trait aux cellules, aux organismes, aux populations, aux écosystèmes ou aux processus qui influent sur les systèmes de production aquatique. Ils doivent aboutir à des conclusions ou synthèses précises qui, de diverse façons, peuvent accroître, modifier, remettre en question ou réorienter le bagage actuel de connaissances et perceptions dans une discipline donnée des sciences aquatiques. Ils doivent clairement démontrer qu'ils contribuent aux connaissances en faisant plus de corroborer des faits. L'originalité doit dépasser le caractère particulier (une année, un endroit, un taxon ou un composé chimique donnée) et tenir à une épuration ou une reformulation des connaissances actuelles.

Les auteurs doivent adresser leurs **manuscrits** à **D.G. Cook**, Journal canadien des sciences halieutiques et aquatiques, Presses scientifiques du CNRC, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada (613-993-2209); télécopieur : 613-952-7656; courrier électronique : journal.cjfas@nrc.ca).

Les contributions peuvent être en anglais ou en français. Elles doivent être originales, c.-à.-d. qu'elles ne doivent pas avoir fait l'objet d'un copyright, avoir été publiées ou soumises ailleurs, sauf sous forme abrégée ou avec le consentement du rédacteur. Le CNRC ne se tient en aucune façon responsable des opinions exprimées par un collaborateur ou des déclarations qui pourrait faire ce dernier. La publication d'annonces publicitaires, d'avis et autres n'implique pas l'endossement de leur contenu par les directeurs du *Journal* ou du CNRC. L'utilisation des noms de marques de commerce ne signifie aucunement une sanction du produit en question ou de la compagnie qui le fabrique.

La correspondance ayant trait aux manuscrits acceptés et les **épreuves corrigés** doivent être envoyées aux Presses scientifiques du CNRC, Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada.

Recommandations aux auteurs sont publiés une fois par année dans le premier numéro de chaque volume. Des copies, ainsi que la **Politique de publication**, sont disponibles auprès des Presses scientifiques du CNRC ou au site Web :
http://www.nrc.ca/cisti/journals/rj.html

Microfilms : On peut acheter sur microfilms de 16 ou 35 mm tous les numéros depuis 1934. Des photocopies d'articles ou de numéros individuels sont aussi en vente auprès de University Microfilms International, 330 North Zeeb Road, Ann Arbor, MI 48106, É.-U.

This journal is indexed or abstracted in / Ce journal est signalé ou résumé dans
Aquatic Sciences and Fisheries Abstracts, Biological & Agricultural Index, CAB Abstracts (Centre for Agriculture and Biosciences), Chemical Abstracts, Current Awareness in Biological Sciences, Current Contents, FAO Freshwater and Aquaculture Contents Tables, FAO Marine Science Contents Tables, GEOBASE – Geo Abstracts, Meteorological and Geoastrophysical Abstracts, Oceanic Abstracts, Science Citation Index, Biological Abstracts, Environment Abstracts, Environmental Periodicals Bibliography, GEOREF, Life Sciences Collection, and PASCAL Database

Volume 54, Supplement 1, 1997

Canadian Journal of Fisheries and Aquatic Sciences

Published by the National Research Council of Canada

Volume 54, supplément 1, 1997

Journal canadien des sciences halieutiques et aquatiques

Publié par le Conseil national de recherches du Canada

Editor / directeur scientifique D.G. Cook

Assistant to the Editor / adjointe au directeur scientifique **M.M. Milne**

Consulting Editor / rédacteur-conseil **P.E.K. Symons** (Victoria, B.C.)

Consulting Editor / rédactrice-conseil **N. Moir** (Nepean, Ont.)

Editorial Board / conseil des rédaction

S.E. Campana, *DFO/MPO, Dartmouth*
E.M.P. Chadwick, *DFO/MPO, Moncton*
L.M. Dickie, *DFO/MPO, Dartmouth*
G.S. Jamieson, *DFO/MPO, Nanaimo*
J.R.M. Kelso, *DFO/MPO, Sault Ste. Marie*
K.R. Munkittrick, *DoE/MdE, Burlington*
J.D. Neilson, *DFO/MPO, St. Andrews*
D.L.G. Noakes, University of Guelph
L.S. Parsons, *DFO/MPO, Ottawa*
R.M. Peterman, *Simon Fraser University*
R.D. Robarts, *DoE/MdE, Saskatoon*
J.C. Roff, *University of Guelph*
D.M. Rosenberg, *DFO/MPO, Winnipeg*
P. Schwinghamer, *DFO/MPO, St. John's*
(Deputy editor / rédacteur adjoint)
C.J. Walters, *University of British Columbia*
W.G. Warren, *DFO/MPO, St. John's*
N.H.F. Watson, *DFO/MPO, Halifax*

NRC Research Press / Presses scientifiques du CNRC

Editor-in-chief / directeur général **Bruce P. Dancik**

Assistant Editor-in-chief / directeur général adjoint **Iain E.P. Taylor**

Journals Program / Programme des revues

(Fax / télécopieur : 613-952-7656; e-mail / courrier électronique : research.journals@nrc.ca;
URL: http://www.nrc.ca/cisti/journals/)

Director / directrice **Aldyth Holmes**

Business Manager / gestionnaire des affaires **Paul McClymont**

Manager, Journals Program / gestionnaire, Programme des revues **Susan R. Strahlendorf**

Senior Publication Officer / agent principal de publication **Mike Boroczki**

Publication Officers / agentes de publication **Jennifer Douglas (613-993-0368), Jennifer McColl (613-993-4500)**

Publication Officer (French manuscripts) / agente de publication (manuscrits français) **Ginette Fortier (613-993-9117)**

Advertising / annonces publicitaires **Hoda Jabbour (613-993-9085)**

Reprints / tirés à part **Judy Heyman (613-993-0151)**

Subscriptions / abonnements **Helen Goulet (613-993-9084)**

© National Research Council of Canada 1997. World rights reserved.

No part of this publication may be reproduced, stored, or transmitted in any form or by any means, without the written permission of the publisher, except as stated below.

The National Research Council of Canada grants **permission*** to individuals to make single copies of articles for personal use. Any person may reproduce short excerpts from articles in the journal for any purpose that respects the moral rights of authors, provided that the source is fully acknowledged. As a courtesy, the consent of authors of such material should be obtained directly from the author.

Authorization to reproduce items for other than personal use, as stated above, is granted by the National Research Council of Canada provided that the copyright fee of $7.00 per copy is paid directly to the Copyright Clearance Center (CCC) Transactional Reporting Service, 21 Congress Street, Salem, MA 01970, U.S.A. 0706-652x/97 $7.00 + 0.00.

*The above permission does not extend to other kinds of copying, such as copying for general distribution, for advertising, or promotional purposes, for creating new collective works, or for resale. For such copying, arrangements must be made with the publisher, National Research Council of Canada, Ottawa, ON K1A 0R6, Canada.

© Conseil national de recherches du Canada 1997. Tous droits réservés.

Il est interdit de reproduire, de sauvegarder ou de transmettre quelque partie de la présente publication dans quelque format ou de quelque façon sans le consentement écrit de l'éditeur, à l'exception des conditions suivantes.

Le Conseil national de recherches du Canada accorde aux particuliers le droit de faire des copies individuelles pour leur usage personnel. Toute personne peut reproduire de courts extraits des articles de la Revue pour autant que les droits moraux de l'auteur soient respectés et que la mention de provenance soit clairement indiquée. Il est de convenance de demander le consentement de l'auteur avant de faire mention de son travail.

On obtiendra l'autorisation de reproduire des articles à d'autres fins que l'usage personnel (tel qu'on l'a décrit ci-dessus) auprès du Conseil national de recherches du Canada pour autant que des redevances de droits d'auteurs de 7,00 $/copie soient versées au Copyright Clearance Center (CCC) Transactional Reporting Service, 21 Congress Street, Salem, MA 01970, U.S.A. 0706-652x/97 7,00 $ + 0,00.

*La permission ci-dessus ne s'applique pas à la reproduction à grande échelle, telle que la reproduction aux fins de distribution générale, publicitaire ou promotionnelle, de compilation de nouveaux ouvrages collectifs ou de revente. Dans de tels cas, il faudra ratifier une entente particulière avec l'éditeur, le Conseil national de recherches du Canada, Ottawa, ON K1A 0R6, Canada.

Subscription information

The *Canadian Journal of Fisheries and Aquatic Sciences* (ISSN 0706-652X) is published monthly by the National Research Council of Canada. 1997 annual subscription rates (second class postage) for Canada are $461CAN institutional and $157CAN personal, for US & foreign $461US institutional and $167US personal. For air mail add $150US to foreign rate. Canadian customers please include 7% GST (business no. 12149 1807 RT 0275). In Quebec please add a further 6.5% QST to the total price including GST (QST no. 1006178088). Subscriptions are entered for the calendar year. Remittances should be made payable to the Receiver General for Canada credit NRC. Price for regular single issues: institutional, $60.00; personal, $25.00. Supplements will be priced separately. Special rates apply to members of Canadian scientific and engineering societies if they subscribe through their respective societies.

There are no refunds on cancelled subscriptions once delivery has begun. Claims for missing issues should be made within four months (N. America) or six months (outside N. America) following the date of publication. The publisher expects to supply missing issues only when losses have occurred in transit and when the reserve stock will permit. For change of address and subscription enquiries: Subscription Office, NRC Research Press, National Research Council Canada, Ottawa, ON K1A 0R6, Canada; tel: 613-993-9084; fax: 613-952-7656; e-mail: research.journals@nrc.ca.

Microform backfiles are available from UMI, P.O. Box 1346, Ann Arbor, MI 48106-1346, U.S.A., and Micromedia Ltd., 20 Victoria St., Toronto, ON M5C 2N8, Canada.

Renseignements sur l'abonnement

Journal canadien des sciences halieutiques et aquatiques (ISSN 0706-652X) est une publication mensuelle du Conseil national de recherches du Canada. Le prix de l'abonnement annuel au Canada (courrier de deuxième classe) est de 461 $CAN pour les organismes et de 157 $CAN pour les particuliers. À l'étranger (y compris les É.-U.), le prix de l'abonnement est de 461 $US pour les organismes et de 167 $US pour les particuliers. L'expédition par avion exige des frais de 150 $US en sus du prix d'abonnement à l'étranger. Les clients du Canada doivent ajouter la TPS de 7% (numéro d'entreprise 12149 1807 RT 0275). Au Québec, il faut ajouter la TVQ de 6,5% au prix total, TPS comprise (n° de TVQ 1006178088). Les abonnements sont pour l'année civile. Tout paiement doit être adressé au Receveur général du Canada, crédit du CNRC. Le prix par numéro est de 60 $ pour les organismes et de 25 $ pour les particuliers. Le prix des hors-série varie. Les membres des sociétés canadiennes de sciences et de génie bénéficient de taux préférentiels en s'abonnant via leurs sociétés respectives.

Aucun remboursement ne sera accordé ni aucune annulation acceptée une fois que les livraisons auront commencé. Les réclamations de numéros manquants devront être soumises dans les quatre mois (Amérique du Nord) ou dans les six mois (à l'extérieur de l'Amérique du Nord) suivant la date de publication. L'éditeur ne fournira de numéros manquants que si le document a été perdu pendant l'expédition et que si le stock le permet. Adressez tout changement d'adresse ou toute question quant à l'abonnement au : Bureau des abonnements, Presses scientifiques du CNRC, Conseil national de recherches Canada, Ottawa, ON K1A 0R6, Canada; téléphone : 613-993-9084; télécopieur : 613-952-7656; courrier électronique : research.journals@nrc.ca.

On peut obtenir les fichiers rétrospectifs sur **microforme** auprès de UMI, P.O. Box 1346, Ann Arbor, MI 48106-1346, É.-U., et auprès de Micromedia Ltée, 20 rue Victoria, Toronto, ON M5C 2N8, Canada.

Selected Proceedings of the Symposium on the Biology and Ecology of Northwest Atlantic Cod

St. John's, Nfld.
October 1994

Sélection de comptes rendus du Symposium sur la biologie et écologie de la morue franche du nord-ouest

St. John's (T.-N.)
octobre 1994

Special Editors/Directeurs scientifiques spéciaux

J.S. Campbell
Department of Fisheries and Oceans, St. John's, Nfld.

P. Schwinghamer
Department of Fisheries and Oceans, St. John's, Nfld.

P.E.K. Symons
Victoria, B.C.

Introduction to the Northwest Atlantic Cod Symposium

J. Scott Campbell

The papers appearing in this supplement are some of those presented at the Symposium on the Biology and Ecology of Northwest Atlantic Cod which was held at the Delta St. John's Hotel in St. John's, Newfoundland, from 24 to 28 October 1994. With two major specially-funded fisheries research programs being concluded, it seemed timely that a symposium should be held to review recent research in federal fisheries laboratories and universities in eastern Canada on Atlantic cod (*Gadus morhua*) and its marine environment. In particular, research results produced under the auspices of the Government of Canada's Northern Cod Science Program (NCSP) and the government/industry-funded Ocean Production Enhancement Network (OPEN) program were to be presented. The goal of the Symposium was to summarize the current knowledge on Atlantic cod biology and ecology with emphasis on the Northwest Atlantic and provide a forum for application of recent research results in addressing specific fisheries problems. The following papers were selected, in keeping with the overall policies of this *Journal*, for their original contributions to our knowledge of the life history, physiology, population dynamics, habitat, and interspecific interactions of Atlantic cod.

The NCSP itself was designed as an intensive 5-yr (1990–1995) fisheries science effort established, and funded to a total of about $28 million, to improve our knowledge of the basic biology and environment of the northern (NAFO Div. 2J and 3KL) Atlantic cod stock. The Program consisted of 25 study initiatives, involving about 50 fisheries and oceanographic researchers in Atlantic Canada and it provided funding for studies on cod reproduction, growth, migration, distribution and diet, and new initiatives in seal abundance, movements, and diet. A major effort in physical oceanography expanded the data base and clarified the broad features of the physical environment off Newfoundland and Labrador. Research in hydroacoustic and survey gear technology was funded to enhance development of systems to add to the tools available to fisheries science in the future.

Related studies on the vital parameters of Atlantic cod were also conducted in the OPEN (1990–1994) program. OPEN was established to investigate the processes that control survival, growth, reproduction, and distribution of fish and shellfish, principally Atlantic cod and scallops. With respect to Atlantic cod, OPEN focussed on recruitment, distribution, physiology, marine genetics, and coastal ocean dynamics. The OPEN research program consisted of 33 projects involving researchers at eight universities and the Department of Fisheries and Oceans with funding totalling about $20 million over the 4-yr period.

The Symposium was attended by over 180 scientists and fisheries specialists from Department of Fisheries and Oceans science branches and from universities in Atlantic Canada. The Symposium was organized into eight sessions where 80 papers were orally presented and 30 papers displayed by poster. The sessions were most ably chaired as follows: Recruitment and Early Life History (Michael M. Sinclair); Physiology (Garth L. Fletcher); Coastal Oceanography (Keith R. Thompson); Population Identification and Characterization (Chris T. Taggart); Growth, Feeding, Predation, and Behaviour (E. Michael Chadwick); Distribution and Population Dynamics (Kenneth T. Frank); Fisheries and Monitoring (D. Bruce Atkinson); Poster Session (M. Ben Davis).

I wish to thank the other members of the Steering Committee, namely Larry W. Coady, George A. Rose, and Kevin M. Keough, and gratefully acknowledge the assistance provided by the local organizing committee made up of Crystal Delaney, Jim Helbig, Larry Jackson, Pierre Pepin, Michelle Roberge, and Joe Wroblewski.

Financial support for the Symposium was provided by the Department of Fisheries and Oceans, the Ocean Production Enhancement Network, and the Office of Research, Memorial University of Newfoundland.

Received September 13, 1996. Accepted September 13, 1996.
J13647

J.S. Campbell. Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

© 1997 NRC Canada

Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*)

P. Pepin, D.C. Orr, and J.T. Anderson

Abstract: We report on the effect of temperature and egg diameter on the development rates of Atlantic cod (*Gadus morhua*) eggs and yolk-sac larvae from experiments in which individuals were followed from fertilization until death. Temperature was the only variable to consistently and significantly affect development rates. Egg size had no consistent effect on transition times during the egg phase, but there was a significant increase in the time to yolk absorption as well as the time until death with increasing egg diameter. Larval length at hatch was significantly greater in larger eggs, but only a small proportion of the variance in length at hatch was explained by egg size (6%). Increasing temperature resulted in a significant increase in the size at hatch and may reflect the overall metabolic load placed on the embryo as temperatures decrease below 1–2°C.

Résumé : Nous rendons compte des effets qu'ont la température et le diamètre de l'oeuf sur le taux de développement des oeufs et des larves vésiculées de la morue franche (*Gadus morhua*), à partir d'expériences qui consistaient à suivre des individus depuis la fécondation de l'oeuf jusqu'à la mort. La température est la seule variable à avoir affecté régulièrement et de façon significative les taux de développement des oeufs. La taille de l'oeuf n'a pas eu d'incidence régulièrement observable sur les périodes de transition au cours de la phase de l'oeuf; par contre, nous avons observé qu'une augmentation du diamètre de l'oeuf entraînait une augmentation significative du temps écoulé jusqu'à la résorption du vitellus, de même que jusqu'à la mort. La longueur des larves à l'éclosion était plus importante pour les oeufs de plus grande taille et ce, de façon significative, mais seule une faible part de la variance observée dans la taille à l'éclosion s'expliquait par la taille de l'oeuf (6%). Une hausse de la température a entraîné une augmentation significative de la taille à l'éclosion, ce qui pourrait refléter la charge métabolique globale que subit l'embryon lorsque les températures baissent au-dessous de 1–2°C.
[Traduit par la Rédaction]

Introduction

Early development of poikilotherms is determined by factors that limit the rate of biological production, the total amount of energy allocated to each offspring, and the interaction between these components which ultimately defines the overall conversion efficiency. Development of the nonfeeding early life stages of fish is significantly influenced by both temperature and egg size (Pauly and Pullin 1988; Pepin 1991). Increased temperature, within the optimal range for a species, results in faster development, and increased egg diameter results in longer times to hatch and increased larval size (Pepin 1991). Intraspecific studies have also noted a strong relationship between the size of eggs and the temperature of the environment in which they are spawned (Blaxter and Hempel 1963; Bagenal 1969; Ware 1975). Ecological and evolutionary arguments suggest that these relationships may represent an adaptation of different stocks or species to their available food resources (e.g., Ware 1975). Such relationships are also believed to extend within the spawning season of individual stocks because of the observations that egg size decreases as the environmental temperature increases (e.g., Ware and Lambert 1985; Miller et al. 1995).

Although the apparent consistency of the size–temperature relationships between and within stocks suggests that increased body size is beneficial in colder temperatures and that this principle applies even at the individual level (Pauly and Pullin 1988; Pepin 1991), the lack of supporting laboratory observations limits the rigour of such an extrapolation (Pepin and Miller 1993). The significance of body size to physiological processes during the egg and larval stages is well established (e.g., Miller et al. 1988; Houde 1989; Pepin 1991) as is the variability in offspring size among females (e.g., Chambers et al. 1988; Kjesbu 1989; Buckley et al. 1991) and in relation to differences in environmental conditions (e.g., Blaxter and Hempel 1963; Bagenal 1969; Ware 1975; Ware and Lambert 1985; Miller et al. 1995). However, because environmental temperature and egg size are correlated, it is difficult to determine the influence that each variable has on the development and potential survival of eggs and larvae. Only under laboratory conditions is it possible to make strong inferences (sensu Platt 1964) about the influence of temperature and size on the development of fish eggs and larvae.

The following study was designed to determine the effects of incubation temperature and initial size on the development (e.g., time to hatch, yolk absorption, starvation) and charac-

Received February 15, 1995. Accepted January 8, 1996.
J13306

P. Pepin, D.C. Orr, and J.T. Armstrong. Department of Fisheries and Oceans, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

© 1997 NRC Canada

Table 1. Description of egg stages as defined by Laurence and Rogers (1976) and Markle and Frost (1985).

Laurence and Rogers 1976	Markle and Frost 1985
Stage I From fertilization until the formation of a complete blastodermal cap	Stage I From fertilization until the visible formation of an embryonic axis about the midgastrula.
Stage II From the formation of a complete blastodermal cap through the development of the segmentation cavity to the first appearance of the germinal ring and embryonic axis	Stage II From the formation of the embryonic axis until the embryo is halfway around the yolk, approximately the time of blastopore closure
Stage III From the first appearance of the germinal ring and embryonic axis to the closure of the blastopore	Stage III From the end of stage II until the tip of the tail reaches or could reach the snout
Stage IV From the closure of the blastopore to hatching	Stage IV From the end stage III until hatching

teristics of individual eggs and yolk-sac larvae of Atlantic cod (*Gadus morhua*). The range of temperatures was chosen to reflect those that occur during the spawning of cod on the northeast Newfoundland shelf (Templeman 1981). We use event analysis to ascertain the effects of temperature and body size on the timing of developmental stages, as suggested by Chambers and Leggett (1989), which provides a method for determining treatment effects on event dispersion.

Materials and methods

Experimental protocol

A broodstock of 30–50 adult cod (40–80 cm TL) was maintained under natural light and temperature regimes at the Ocean Sciences Centre, Memorial University, St. John's, Nfld. The fish had been captured using a bottom trawl and held in captivity for at least 6 mo during which time they were fed a mixture of dry feed and capelin (J.A. Brown, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada, personal communication). The physiological condition of fish during the spawning season was not recorded. Eggs and sperm were collected from two to four ripe female and three to five running male cod. Only females that yielded eggs freely (i.e., with little or no pressure on the vent) were used in these experiments. We did not determine if the same individuals were used in the different experimental trials of this study. Eggs and sperm were combined in filtered seawater at ambient temperature (1–3°C). After approximately 6 h postfertilization, 150 viable zygotes were separated into individual 30-mL sterile vials filled with UV-sterilized filtered (0.45 μm) seawater. Thirty vials were transferred to each of five water baths which were maintained at −1, 1, 3, 5, or 7°C using Neslab RTE-220 flow-through controllers. Seawater in each vial was replaced every 2 d throughout the experiment. Eggs were treated with a solution containing 100 mg streptomycin·L^{-1} and 60 mg penicillin·L^{-1}. Vials were checked daily to determine the stage of development, as described below. The experiment was repeated three times starting on 1 May 1991, 9 May 1991, and 23 May 1991.

To extend our analysis beyond events associated with the larval stage (i.e., hatch, yolk absorption, death), two descriptive staging schemes were used to monitor development during the egg stage. Each scheme divides development of the egg into four stages (Table 1). The scheme used in all experimental trials was that of Laurence and Rogers (1976), which has similarities to that of Thompson and Riley (1981). During the third experimental trial, we also used the staging scheme of Markle and Frost (1985). The former scheme places greater emphasis on separation of the early developmental stages whereas the latter provides a more even separation of stages through the period from fertilization until hatch. Both schemes provide information that permits age determination of field sampled eggs, given environmental temperatures and information on development rates. In both schemes, the end of stage IV represents hatch. In addition to the time until the end of the four egg stages, we noted the time until yolk absorption as well as time of death. Death occurred during all stages of development and was due principally to developmental abnormalities during the egg stage, and to the exhaustion of energy reserves during the larval stage.

During the second and third trials, individual egg diameter on the day of fertilization and length of the larva at hatch were measured to the nearest 0.1 mm using an image analysis system mounted on a Wild M3C dissecting microscope with an S-type mount fitted with a 0.5× objective.

Analysis

The analysis of transition times (i.e., age at the end of a stage) for early life history stages was performed using a technique for event analysis, wherein the entire distribution of event times, rather than only the mean or median, is used to depict the schedule of transitions from one stage to the next. Details of methods for event analysis are available from Cox and Oates (1984) and applications to early life history development were given by Chambers and Leggett (1989).

A Weibull distribution was selected to model event data in this study. The survival function of the Weibull distribution is defined as

$$(1) \quad S(t) = e^{[-(t/\alpha)^{\gamma}]}$$

where t is time, α is the scale parameter in units of time (i.e., days),

© 1997 NRC Canada

and γ is a dimensionless shape parameter. Equation 1 is modified into an accelerated failure time model by including treatment variables, described by a vector $\nu' = (\nu_1, \nu_2, ..., \nu_k)$ such that

$$(2) \quad S(t; \nu) = e^{[-(t/\alpha)^{\gamma} e^{\nu'\beta}]}$$

assuming that the elements of ν interact through a linear function, $\nu'\beta$, where the parameters, β_i's, are estimated.

Analysis involves the logarithmic transformation of event times which yields the standard extreme value distribution that is multiplied by a scale factor (analogous to the variance of a normal distribution) and translated by a location parameter (β). Observations of event times are related to explanatory variables as

$$(3) \quad Y = V\beta + \sigma\epsilon$$

where Y is the vector of ln-transformed event times, V is the matrix of explanatory variables, β is the vector of coefficients to be estimated, σ is the scale parameter to be estimated, and ϵ is the extreme value distribution in the case of the Weibull distribution. In this case, σ is equal to the inverse of the Weibull shape parameter γ. The first column of V is typically a unit vector such that β_1 estimates the intercept which in this context is the location parameter of the extreme value distribution. In equation 3, the explanatory variables act additively on Y, the ln-transformed time, leading to an acceleration or deceleration of event times. The explanatory variables considered in our analysis were temperature and the ln-transformed egg diameter. We transformed egg diameter because we had no a priori expectation that transition times were exponentially related to egg diameter. The effect of sequential trial numbers is excluded from the analysis because of the small number of observations available (i.e., three) relative to the spawning period of individual fish (Kjesbu 1989) and because we used several male and female fish to obtain and fertilize the eggs for each trial. Analysis was performed using maximum likelihood.

The Pth percentile of the cumulative distribution function for age-at-stage transition can be estimated as

$$(4) \quad \hat{y} = \beta_1 + \nu\beta_i + u_p\sigma$$

where $y = \ln(t)$, β_1 is the location parameter, ν are the covariates (temperature and egg diameter) and β_i are their coefficients, σ is the scale parameter of the extreme value distribution, and $u = \ln[-(\ln(1 - P)]$ is the Pth standard extreme value percentile.

The relationships between survival rates and temperature and between egg diameter and larval length were evaluated using general linear models fitted by least squares. Such models were also used as complementary alternatives to event analysis in order to assess the relative effects of egg diameter and temperature on transition times in instances where both were considered to have a significant effect based on maximum likelihood approximations.

Results

Increased temperature led to faster transition times and was the only variable to have a consistently significant effect on development rates of cod eggs and yolk-sac larvae (Table 2). Although there was some variation in the slope of the response of development rates to changes in temperature (Table 2), the effect appeared to have little impact on the uniformity of development among stages at the different temperatures when all experimental trials were combined (Fig. 1). The average ratio of development rates expected for a 10°C change in temperature (Q_{10}) was 3.7. The staging scheme of Markle and Frost (1985) yielded similar results (Q_{10} = 3.9), but because only one experimental trial was available to estimate the parameters, we will restrict all further discussion to the results obtained using the staging scheme of Laurence and Rogers (1976).

Age-at-death was the only process not significantly influenced by temperature (Table 2; Fig. 1). As a result, the distribution of mortalities tended to move towards later stages of development as temperature increased. Consequently, overall survival to hatch was significantly influenced by temperature ($F_{1,12} = 10.9$, $p < 0.01$) (Fig. 2). Despite the scatter, it is clear that mortality to hatch decreases with increasing temperature, within the range of conditions used in these experiments.

Egg diameter had a significant influence on age-at-transition for the stage II eggs only ($\chi_{[1]}^2 = 9.96$, $p < 0.01$). Increasing egg diameter led to longer development times. The age-at-transition for the other egg stages (I, III, IV) was not significantly influenced by egg diameter.

In addition to having no apparently strong and consistent effect on stage-specific transition times during the egg phase, egg diameter did not have a significant effect on the probability of hatching (Fig. 3). Although the two trials for which we had information on egg size had notably different distributions of diameters, we found no evidence of a consistent difference in the probability of hatching for a given size between the two experiments. Furthermore, there was no evidence that the size-dependent probability of hatching changed in relation to temperature.

Although egg diameter had no notable effect on transition times during the egg phase, egg diameter did significantly effect time to yolk absorption ($\chi_{[1]}^2 = 8.64$, $p < 0.01$) (Fig. 4) as well as the age-at-death ($\chi_{[1]}^2 = 7.17$, $p < 0.01$) (Fig. 5; Table 2), both of which increased for larger eggs. If instead of using event analysis we use an ANCOVA to assess the relative effects of temperature (T) and egg diameter (ϕ) on time to yolk absorption (t) ($\ln(t) = a + bT + c\ln(\phi)$, where a, b, and c are parameters to be estimated), we find that egg diameter explains only an additional 3% of the variance in individual development rates ($F_{1,82} = 4.1$, $p < 0.05$) after taking into account the effect of temperature which explains 56% of the variance ($F_{1,82} = 105$, $p < 0.001$). Although temperature did not significantly influence age-at-death ($F_{1,280} = 0.2$, $p > 0.5$), egg diameter explained only 3% of the variance ($F_{1,280} = 9.1$, $p < 0.01$).

Larval length at hatch was significantly positively related to egg diameter ($F_{1,75} = 5.2$, $p < 0.05$). However, as with the effect of egg size on time to yolk absorption or age-at-death, only a small proportion of the variance in length at hatch was explained by egg size (6%) (Fig. 6). Increasing temperature resulted in a significant increase in the size at hatch ($F_{4,75} = 2.53$, $p < 0.05$) resulting in a 1.2-mm increase in average length of larvae for an increase in temperature of 8°C (Fig. 7). We used an ANCOVA where temperature was treated as a classification variable because we had no a priori expectation of the functional form of the relationship between length at hatch and temperature.

The scale parameter of equation 3, σ, which provides a measure of the spread in the distribution of observations, tended to decrease with increasing development. This suggests that the stage-specific transition times were most variable for the transitions from stage I to II and from stage II to III and decreased thereafter as embryos and larvae

© 1997 NRC Canada

Table 2. Stage-specific fit to the accelerated failure time model (equation 3), with ln-transformed observations of transition times for the staging schemes of Laurence and Rogers (1976).

	Parameter estimate	SE	χ^2	$p <$
Stage I				
Location, β_1	2.39	0.13		
Temperature, β_2	-0.17	0.009	371	0.001
Egg diameter, β_3	-0.41	0.35	1.35	0.3
σ	0.36	0.016		
Stage II				
Location, β_1	2.08	0.19		
Temperature, β_2	-0.15	0.015	108	0.001
Egg diameter, β_3	1.59	0.50	10.2	0.01
σ	0.43	0.020		
Stage III				
Location, β_1	2.70	0.12		
Temperature, β_2	-0.13	0.009	215	0.001
Egg diameter, β_3	0.12	0.31	0.14	0.8
σ	0.24	0.013		
Stage IV				
Location, β_1	3.56	0.075		
Temperature, β_2	-0.13	0.007	389	0.001
Egg diameter, β_3	0.15	0.19	0.63	0.5
σ	0.13	0.011		
Yolk Abs.				
Location, β_1	3.84	0.099		
Temperature, β_2	-0.16	0.012	152	0.001
Egg diameter, β_3	0.67	0.23	8.87	0.01
σ	0.11	0.008		
Mortality				
Location, β_1	2.15	0.22		
Temperature, β_2	0.021	0.017	1.62	0.3
Egg diameter, β_3	1.66	0.61	7.36	0.01
σ	0.74	0.034		

Note: The equation was fit to the combined data from the three experimental trials. Egg diameter was ln-transformed. The χ^2 statistic tests the null hypothesis of no effect of temperature (i.e., $\beta_2 = 0$) or egg diameter (i.e., $\beta_3 = 0$) with df = 1.

approached the time to hatch and of yolk absorption (Fig. 8), respectively.

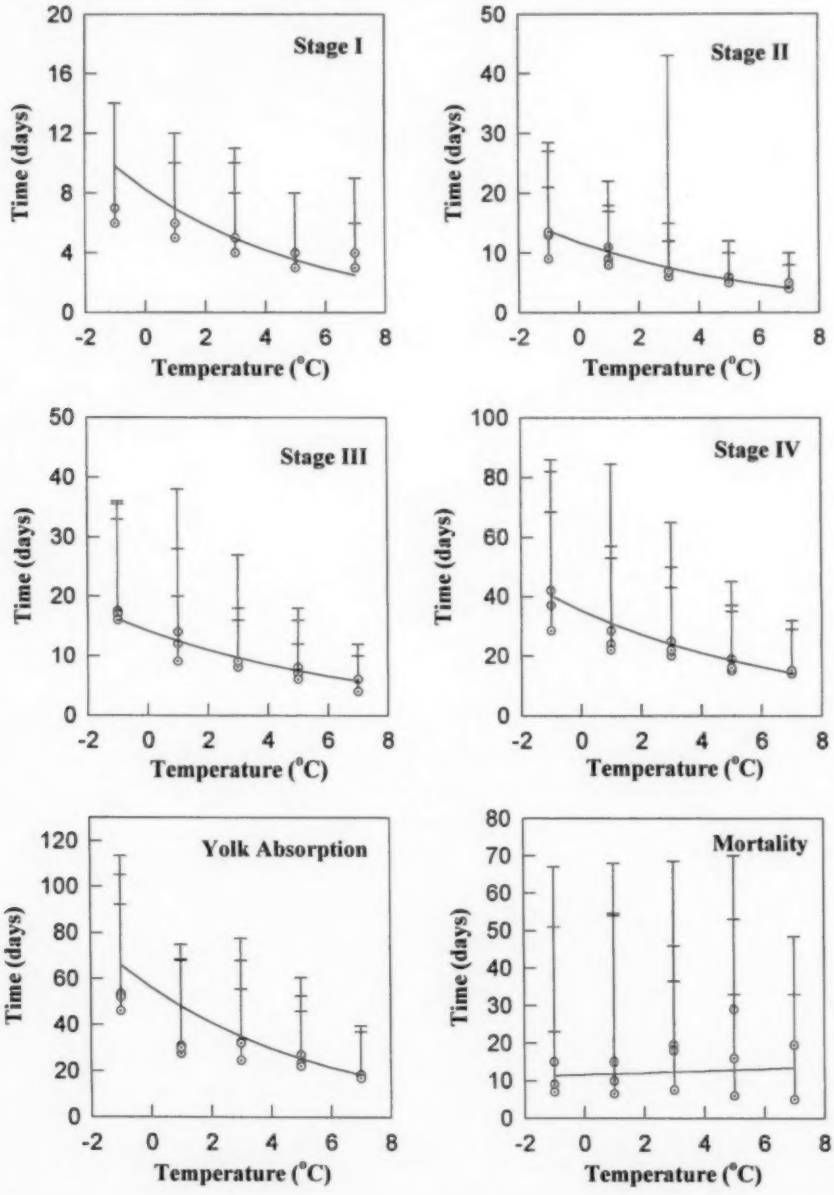
Discussion

Temperature proved to have a greater influence on development rates of cod eggs and yolk-sac larvae than egg size. Although there is evidence that metabolic processes, such as respiration rates, increase with increasing body size during embryonic stages (e.g., Davenport and Lønning 1980; Rombough 1988), there may be relatively little impact on development rates caused by the variation in embryo size, at least prior to hatch. As a result, the temperature dependence of the biochemical reactions that govern metabolism is likely to be the dominant factor governing early development in cod. The strong temperature dependence of embryonic development rates may prove to be useful by giving added reliability to ageing of eggs from field collection without having to be overly concerned about possible influences of initial size.

The magnitude of the temperature effect observed in this study shows some disparity with previous work on cod. Data from both Laurence and Rogers (1976) and Thompson and Riley (1981) indicate a Q_{10} of 2.3 and 2.7 in times to hatch, respectively, whereas our results yield a Q_{10} of 3.7, and Page and Frank (1989) obtained a value of 4.6 in their review, which excluded data from Thompson and Riley (1981). Part of the difference in the temperature effect may stem from the lower temperature limit of the different studies. Both Lau-

© 1997 NRC Canada

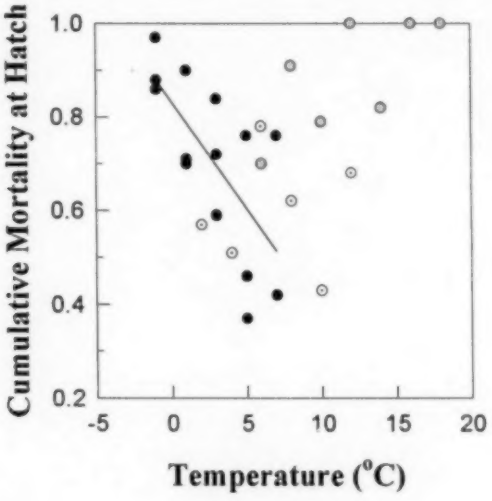
Fig. 1. Estimated age at which 50% of individuals reach the end of individual developmental stage of cod eggs and yolk-sac larvae in relation to temperature for the staging schemes of Laurence and Rogers (1976) (solid line) for the experimental mean egg size of 1.42 mm. Parameters are listed in Table 2. Open dotted symbols represent the 50th percentile of the data for each experimental trial and the capped error bar represents the range up to the 95th percentile of the data. Note that the fitted relationships were based on the distribution of number of individuals that transited each stage at each temperature regime and not on a single estimate of location for each experimental trial.



rence and Rogers (1976) and Thompson and Riley (1981) limited their experiments to temperatures of 2°C or more. Page and Frank's (1989) fig. 6 indicates a sharp discontinuity in the rate of increase in hatch times at temperatures below 2°C, largely due to works by Earll (1878), Dannevig (1895), and Brice (1898). These results would suggest that the lower limit of thermal tolerance in the development of cod eggs may occur at temperatures below 1–2°C. However, we found no evidence of such a sharp discontinuity in our general analysis (Fig. 1). This may reflect local adaptations to environmental conditions due to genetic isolation of cod on the northeast Newfoundland Shelf from other stocks (Carr and Marshall 1991), but further research is required to properly address this issue. Alternatively, this may reflect differences

© 1997 NRC Canada

Fig. 2. Cumulative mortality to 50% hatch in relation to temperature from this study (solid symbols). The solid line represents the least squares regression line $Y = 0.83 - 0.046X$, where Y is the cumulative mortality to 50% hatch and X is temperature. Each point represents an experimental trial. Data from Laurence and Rogers (1976) (open dotted symbols) and Iversen and Danielssen (1984) (shaded symbols) are included for comparison (see discussion).

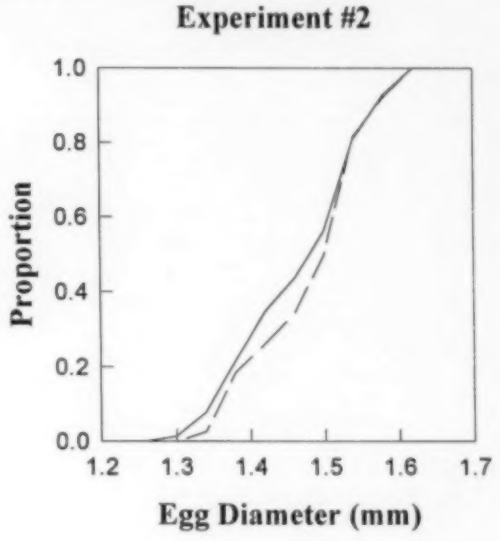


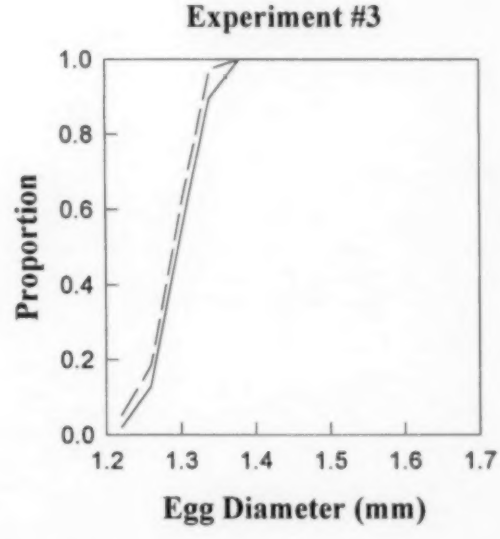
in experimental or analytical approaches between this and earlier studies.

We have demonstrated that cod eggs from the northeast Newfoundland shelf stock can develop normally at ocean temperatures as low as −1°C although there was high mortality during early development. This extends the lower tolerance limit for normal development in this species. In comparison, Thompson and Riley (1981) found that death occurred in the early stages of cleavage at temperatures below 1.5°C in cod from the southern North Sea. Although we found mortality increased with decreasing temperatures, a comparison with work by Laurence and Rogers (1976) and Iversen and Danielssen (1984) suggests that the cumulative mortality during development reaches a minimum in the 5–10°C range and increases above and below that (Fig. 2). The implication is that for cod eggs on the northeast Newfoundland Shelf, production early in the spawning season, before surface waters have warmed, can lead to low overall survival during this stage of development.

Although egg size did not have an important influence on development during the egg stage, there was a significant effect on the characteristics of yolk-sac larvae. As in previous studies (e.g., Blaxter and Hempel 1963; Chambers et al. 1988; Buckley et al. 1991), body length at hatch was correlated with egg size but this relationship was weak. However, our observations are consistent with Miller et al.'s (1995) results which showed that the egg – larval size relationship was highly variable within surveys of cod on the Scotian Shelf. They noted that a stronger egg – larval size relationship was obtained when data from a broad range of environmental conditions were combined. A similar contrast with previous studies was apparent when we considered the relationship

Fig. 3. Cumulative distribution of egg diameters at the start of the second and third experimental trials (solid line) and of the eggs that successfully hatched (broken line).





between egg diameter and time to yolk absorption. Although Blaxter and Hempel (1963) found that increased egg size is associated with a longer time until endogenous resources are completely utilized, our results indicate that the overall effect of individual egg size was weak. Much of the contrast between our findings and previous studies may arise from the basis for comparison. Many of the principles pertaining to the effects of both egg and larval size on physiological processes during the early life history of fish are derived from a comparison of group averages or distributions, whether these groups represent species, stocks of a species, or families within stocks (Pepin and Miller 1993). We focus on the vari-

© 1997 NRC Canada

Fig. 4. Relationship between time to yolk absorption and egg diameter. The key indicates the temperatures at which the eggs were incubated. The broken line shows the expected time to 50% yolk absorption, based on maximum likelihood estimates (Table 2), in relation to egg diameter. The line is based on the average overall mean temperature of 4.7°C, estimated for all the observations shown (n = 83).

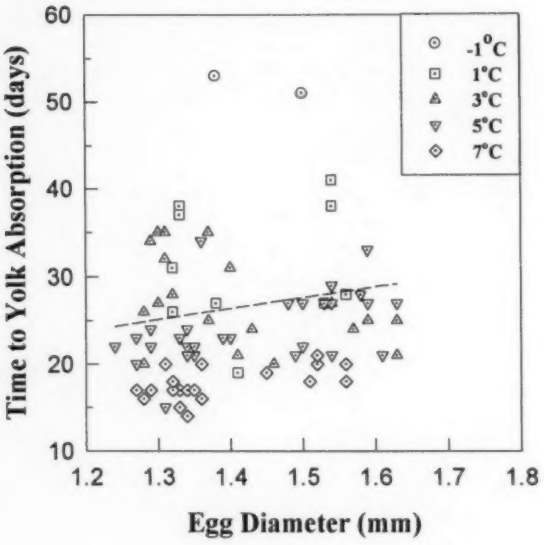


Fig. 5. Relationship between the age-at-death and egg diameter. The key indicates the temperatures at which the eggs were incubated. The broken line shows the expected time to 50% death, based on maximum likelihood estimates (Table 2), in relation to egg diameter. The line was based on an average overall mean temperature of 2.7°C, estimated for all the observations shown (n = 281).

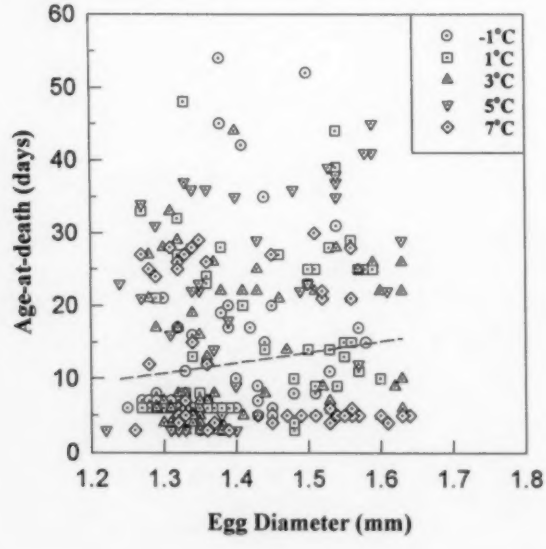
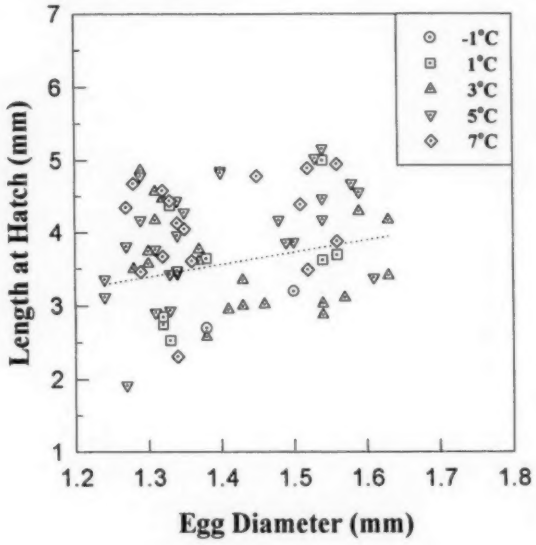


Fig. 6. Relationship between length at hatch of cod larvae and the diameter of the egg. The legend indicates the temperatures at which the eggs were incubated. The dotted line represents the expected length at hatch, estimated for a temperature of 3°C using an ANCOVA in which temperature was treated as a classification variable, in relation to egg diameter.



ability among individuals produced under similar conditions. Thus, we reduce potentially confounding factors, such as differences in physiological history of individual parents or gross differences in environmental conditions, that may lead to size-correlated trends in developmental features without necessarily having a size-dependent influence on the individual larva. We propose that the effect of body size on the early development characteristics of fish may in fact be substantially less important than previously suggested. It is possible that much of the variance in size-dependent developmental constraints of eggs and yolk-sac larvae may represent the overall influence of environmental features characteristic of spatial or temporal variations within or among ecosystems.

The effect of both temperature and egg size on the length of larvae at hatch was an unexpected finding of our study. Ware and Lambert (1985) noted a strong negative relationship between the average size of fish eggs and the temperature of the environment in which the eggs are caught. As well, Miller et al. (1995) found a strong positive relationship between the size of cod larvae and the egg from which each individual hatches. The conclusion from such studies has been that large eggs are produced in colder waters and yield larger larvae. Our results indicate that for a restricted number of experimental trials, the relationship between size at hatch and temperature is opposite to that noted under field conditions by Miller et al. (1995). Part of the contrast may be due to the generally weak relationship between egg size and size at hatch noted within experiments (this study) or within sampling periods (Miller et al. 1995). The inverse relationship between size at hatch and incubation temperature obtained in this study may be the result of the overall metabolic load placed on the

© 1997 NRC Canada

Fig. 7. Estimated average larval standard length at hatch in relation to temperature. The error bars represent standard errors estimated from an ANCOVA in which temperature was treated as a classification variable. The average egg size used for the estimate was 1.42 mm.

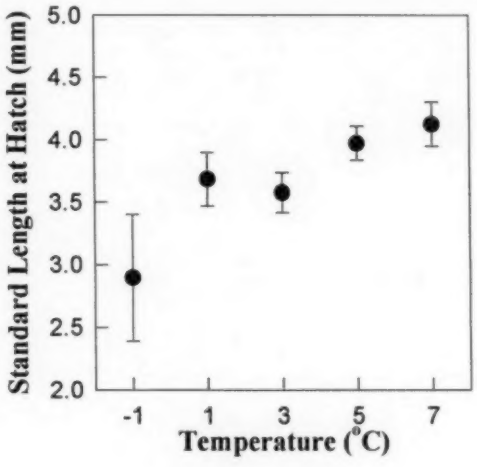
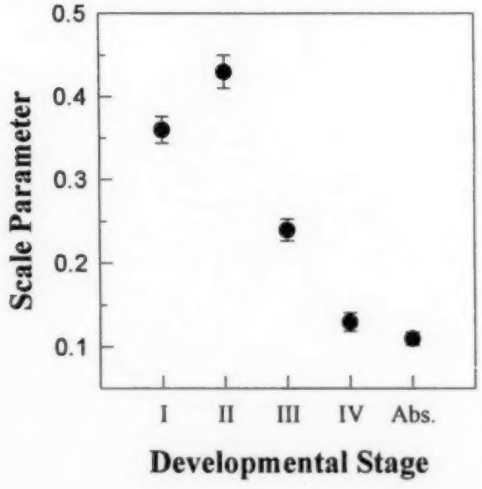


Fig. 8. Scale parameter (σ), with estimated standard errors, in relation to developmental stage from which cod eggs or larvae were transiting. The end of stage IV corresponds to hatch.



embryo as temperature decreases. The Q_{10} of decreasing incubation time with increasing temperature from this and previous studies (Laurence and Rogers 1976; Thompson and Riley 1981; Page and Frank 1989) ranges from 2.3 to 4.6 (average = 3.3). This contrasts with an average Q_{10} of 2.7 for the increase in respiration rate (micrograms O_2 per gram weight per hour) with increasing temperature for nonsalmonid species listed in Rombough's (1988, table IV) review. The implication is that the overall metabolic load (i.e., total respiration from fertilization to hatch) increases with decreasing temperature. This would result either in smaller energy reserves or a smaller individual at hatch for a given egg size. Alternatively, differences in the effect of temperature on developmental characteristics may occur in different populations or over a broader range of conditions. Chambers et al. (Huntsman Marine Science Centre, St. Andrews, NB E0G 2X0, Canada, personal communication) observed a dome-shaped relationship in the average length at hatch, for a given average egg diameter, in relation to incubation temperature. The range of temperatures used in this study corresponds to the lower range of conditions in Chambers' (personal communication) treatments whereas the average conditions encountered during Miller et al.'s (1995) surveys correspond to the middle to upper range used by Chambers. Consequently, the contrasting results observed in this and Miller et al.'s (1995) study may represent observations along the ascending and descending limb of a dome-shaped relationship between length at hatch and environmental temperature. The paucity of information pertaining to the determinants of egg size in highly fecund fish does not permit us to reject any hypothesis that could reconcile the contrast between field and laboratory observations of the relationship between egg diameter, temperature, and length at hatch. It appears that one must be cautious in the interpretation of relationships between body size and environmental factors unless the functional response has been carefully established over the full range of conditions that a species may encounter.

Acknowledgements

We thank C. Bishop, J. Morgan, W. Warren, and an anonymous reviewer for their constructive criticism. Assistance from J.A. Brown, J. Ryder, T.H. Shears, D. Somerton, and P.J. Williams was essential to this work. This research was supported by the Northern Cod Science Program (DFO).

References

Bagenal, T.B. 1969. Relationship between egg size and fry survival in brown trout *Salmo trutta* L.J. Fish Biol. **1**: 349–353.

Blaxter, J.H.S., and Hempel, G. 1963. The influence of egg size on herring larvae (*Clupea harengus*). J. Cons. Int. Explor. Mer, **28**: 211–240.

Brice, J.J. 1898. A manual for fish-culture, based on the methods of the United States Commission on Fish and Fisheries. Appendix to U.S. Comm. Fish. Rep. **23**(1897): 1–340.

Buckley, L.J., Smigielski, A.S., Halavik, T.A., Caldarone, E.M., Burns, B.R., and Laurence, G.C. 1991. Winter flounder *Pseudopleuronectes americanus* reproductive success. II. Effects of spawning time and female size on size, composition and viability of eggs and larvae. Mar. Ecol. Prog. Ser. **74**: 125–135.

Carr, S.M., and Marshall, H.D. 1991. Detection of intraspecific DNA sequence variation in the mitochondrial cytochrome *b* gene of Atlantic cod (*Gadus morhua*) by the polymerase chain reaction. Can. J. Fish. Aquat. Sci. **48**: 48–52.

Chambers, R.C., and Leggett, W.C. 1989. Event analysis applied to timing in marine fish ontogeny. Can. J. Fish. Aquat. Sci. **46**: 1633–1641.

Chambers, R.C., Leggett, W.C., and Brown, J.A. 1988. Variation in and among early life history traits of laboratory-reared winter flounder (*Pseudopleuronectes americanus*). Mar. Ecol. Prog. Ser. **47**: 1–15.

Cox, D.R., and Oates, D. 1984. Analysis of survival data. Monographs on statistics and applied probability. Chapman Hall. London.

Dannevig, H. 1895. The influence of temperature on the development of the eggs of fishes. Rep. Fish. Board Scotl. **13**: 147–152.

© 1997 NRC Canada

Davenport, J., and Lønning, S. 1980. Oxygen uptake in developing eggs and larvae of cod, *Gadus morhua*. J. Fish Biol. **16**: 249–256.

Earll, R.E. 1878. A report on the history and present condition of the shore cod fisheries of Cape Ann, Mass., together with notes on the natural history and propagation of the species. U.S. Comm. Fish. Rep. **6**(1878): 685–740.

Houde, E.D. 1989. Comparative growth, mortality, and energetics of marine fish larvae: temperature and implied latitudinal effects. Fish. Bull. U.S. **87**: 471–496.

Iversen, S.A., and Danielssen, D.S. 1984. Development and mortality of cod (*Gadus morhua* L.) eggs and larvae in different temperatures. *In* The propagation of cod *Gadus morhua* L. *Edited by* E. Dahl, D.S. Danielssen, E. Moksnes, and P. Solemdal. Flødevigen Rapp. **1**: 49–65.

Kjesbu, O.S. 1989. The spawning activity of cod, *Gadus morhua* L. J. Fish Biol. **34**: 195–206.

Laurence, G.C., and Rogers, C.A. 1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.). J. Cons. Int. Explor. Mer. **36**: 220–228.

Markle, D.F., and Frost, L.-A. 1985. Comparative morphology, seasonality, and a key to planktonic fish eggs from the Nova Scotian Shelf. Can. J. Zool. **63**: 246–257.

Miller, T.J., Crowder, L.B., Rice, J.A., and Marschall, E.A. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Can. J. Fish. Aquat. Sci. **45**: 1657–1670.

Miller, T.J., Herra, T., and Leggett, W.C. 1995. An individual-based analysis of the variability of eggs and their newly-hatched larvae of Atlantic cod (*Gadus morhua*) on the Scotian Shelf. Can. J. Fish. Aquat. Sci. **52**: 1083–1093.

Page, F.H., and Frank, K.T. 1989. Spawning time and egg stage duration in Northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns Bank. Can. J. Fish. Aquat. Sci. **46**(Suppl. 1): 68–81.

Pauly, D., and Pullin, R.S.V. 1988. Hatching time in spherical, pelagic marine fish eggs in response to temperature and egg size. Environ. Biol. Fishes, **22**: 261–271.

Pepin, P. 1991. The effect of temperature and size on development and mortality rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. **48**: 503–518.

Pepin, P., and Miller, T.J. 1993. Potential use and abuse of general empirical models of early life history processes in fish. Can. J. Fish. Aquat. Sci. **50**: 1343–1345.

Platt, J.R. 1964. Strong inference. Science (Wash., D.C.), **146**: 347–353.

Rombough, P.J. 1988. Respiratory gas exchange, aerobic metabolism, and effects of hypoxia during early life. *In* Fish physiology. Vol. XI. The physiology of developing fish. Part A. Eggs and larvae. *Edited by* W.S. Hoar and D.J. Randall. Academic Press, San Diego, Calif. pp. 59–161.

Templeman, W.T. 1981. Vertebral numbers in Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas, 1947–1971, and their use for delineating cod stocks. J. Northwest Atl. Fish. Sci. **2**: 21–45.

Thompson, B.M., and Riley, J.D. 1981. Egg and larval development studies in the North Sea cod (*Gadus morhua* L.). Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **178**: 553–559.

Ware, D.M. 1975. Relation between egg size, growth and natural mortality of larval fish. J. Fish. Res. Board Can. **32**: 2503–2512.

Ware, D.M., and Lambert, T.C. 1985. Early life history of Atlantic mackerel (*Scomber scombrus*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **42**: 577–592.

© 1997 NRC Canada

Family relationships and effective population size in a natural cohort of Atlantic cod (*Gadus morhua*) larvae

C.M. Herbinger, R.W. Doyle, C.T. Taggart, S.E. Lochmann, A.L. Brooker, J.M. Wright, and D. Cook

Abstract: Sibship relationships within a naturally spawned cohort of Atlantic cod (*Gadus morhua*) larvae on the Western Bank of the Scotian Shelf were investigated by a likelihood ratio method that estimates relationships is among individuals using microsatellite (DNA fingerprint) information. We found no evidence of any temporal or spatial family structure among the larvae from seven different sample collections taken at sequential time intervals during a 21-d period of sampling the larval cohort. There was no evidence that larvae were more related within sample collections than across sample collections. Within each sample collection, there was no evidence of a family structure within or among the depths sampled. Similarly, there was no apparent change in the potential occurrence of sibship with time (successive sample collections), or in association with the passage of a storm during the sampling period. This cohort of cod larvae appears to have been a fairly homogeneous mixture of larvae that were not siblings and came from a large genetic pool. The minimum estimate of the inbreeding effective population size is 2800 individual spawners.

Résumé : Nous avons étudié la proximité génétique au sein d'une cohorte de larves de morue franche (*Gadus morhua*) écloses dans la nature sur le banc ouest de la plate-forme néo-écossaise en utilisant une méthode de rapport des vraisemblances qui permet d'estimer les liens entre individus à l'aide de données fournies par les microsatellites (identification par le code génétique). Nous n'avons pas trouvé d'indication de structures familiales temporelles ou spatiales entre les larves de sept ensembles d'échantillons différents, prélevés à des intervalles de temps séquentiels, au cours d'une période de 21 d de prélèvements dans la cohorte de larves. Il n'y avait pas d'indication que les larves étaient plus proches génétiquement au sein d'un même ensemble d'échantillons que par comparaison aux larves des autres ensembles. À l'intérieur de chaque ensemble d'échantillons, il n'y avait pas d'indication d'une structure familiale à une profondeur donnée ou entre les profondeurs de prélèvement. De même, aucun changement apparent dans la probabilité de proximité génétique n'a été observé au fil du temps (prélèvements successifs d'échantillons), ni par suite du passage d'une tempête au cours de la période d'échantillonnage. Cette cohorte de larves de morue semble avoir été constituée d'un mélange assez homogène de larves qui n'étaient pas liées génétiquement, et qui provenaient d'un réservoir génétique important. La valeur estimative minimale du nombre d'individus requis dans une population pour que se manifeste la proximité génétique est de 2 800 géniteurs.
[Traduit par la Rédaction]

Introduction

It has been proposed that new insights needed to predict recruitment variations in Atlantic cod (*Gadus morhua*) and other marine fish should come from studying, among other phenotypic traits, the genetic traits of the individuals that survive and eventually recruit (Taggart and Frank 1990). Proposals of this kind are derived from evidence that suggests that relatively few of the many cohorts spawned annually may be responsible for ultimate year class strength (e.g., Lambert 1984) and from predictions, based on small scale spatial and temporal heterogeneity in the natural environment, that individual cohorts of larvae should reveal genetic evidence of having been produced by a small part of the potential parental pool (Hedgecock 1994*a*, 1994*b*).

Strong selective mortality between male (sire) half-sibship during the critical transition to exogenous feeding has been demonstrated in laboratory-reared cod larvae (Doyle et al. 1995). However, the extent of familial relationship among individual larvae from naturally spawning populations has so far been nearly impossible to measure. This is particularly true for species where mating behaviour cannot easily be observed. Brawn (1961) observed pair matings and male dominance, and unpaired female spawning as well, in cod maintained in aquaria. However, spawning behaviour in large cod aggregations in nature is still largely unstudied.

Several classes of genetic markers (e.g., allozyme, mitochondrial DNA and nuclear DNA markers) are currently used to address various population genetic problems. One class of such nuclear DNA markers, the microsatellites, exhibits

Received February 24, 1995. Accepted January 16, 1996.
J13439

C.M. Herbinger, R.W. Doyle, J.M. Wright, and D. Cook. Marine Gene Probe Laboratory, Department of Biology, Dalhousie University, Halifax, NS. B3H 4J1, Canada.
C.T. Taggart. Department of Oceanography, Dalhousie University, Halifax, NS. B3H 4J1, Canada.
S.E. Lochmann. Fisheries Biology Program, University of Arkansas at Pine Bluff, Pine Bluff, AK, U.S.A.
A.L. Brooker. Australian Institute of Marine Science, PMB 3 Townsville, M.C. Queensland, Australia 4810.

© 1997 NRC Canada

attributes that make them particularly suitable for fish population genetic research (Wright and Bentzen 1994). Microsatellites are short stretches (10–100 base pairs) of DNA composed of di-, tri-, or tetranucleotide repeats arrayed in tandem (Wright 1993). Each microsatellite locus (i.e., each tandemly arrayed repeat) is flanked by unique DNA sequences. Complementary sequences can be made that hybridize to these unique flanking regions to act as primers for amplification of the tandem array by polymerase chain reaction (PCR). The length of the different size variants of the tandemly repeated array (i.e, the different microsatellite alleles) can then be accurately determined by electrophoresis on a sequencing gel (Wright and Bentzen 1994). Among the attributes that make microsatellites a particularly attractive class of genetic markers are their abundance, their extremely high levels of allelic variation, and the fact that they are codominant markers inherited in a Mendelian way (Wright and Bentzen 1994).

The ability to use genetic marker information to infer relatedness among individuals would be a valuable tool to study natural populations, but it has proved to be a very difficult task. Assessment of parent–offspring relationships from analysis of band sharing in multilocus fingerprints requires a detailed knowledge of the study population and DNA samples from both parents and their offspring (Wetton et al. 1987). Precise estimation of individual relatedness is generally impossible (Lynch 1988). Brookfield and Parkin (1993) examined in a theoretical model the use of hypervariable single-locus DNA probes to provide evidence of relatedness of pairs of individuals from a wild population. They concluded that it should be possible to distinguish siblings from unrelated individuals with a realistically small number of loci.

In this paper, a likelihood ratio method is developed to infer possible half-sib or full-sib relationships from single-locus microsatellite data. The existence of sibships among cod larvae was investigated by this approach on a population that was tracked within a well-defined water mass on the Western Bank of the Scotian Shelf. The motivation for the study was two-fold: (1) to infer the mating structure of the spawning aggregation that produced the cohort and to estimate a lower bound for the effective population size of that spawning aggregation; and (2) if families were detected in the larvae, to see if the action of natural selection among sibship could be directly observed in a naturally spawned cohort of larvae over time, as had been observed in the laboratory.

Material and methods

Field operations and larval collections

The field operations of this study were conducted aboard the MV Petrel V from 22 November to 16 December 1992 in the North Atlantic area 4VsW (Western Bank of the Scotian Shelf).

Tracking of the larval cod cohort was enabled through the use of Ocean Probe, a hardware configuration employed to collect and display data from an array of oceanographic instrumentation and enabling the real-time tracking of a particular water mass (Bowen et al. 1995). The operational design allowed us to sample repeatedly the same water mass throughout the sampling period with the exception of a 4-d period (4–7 December) when a storm curtailed sampling.

Larval cod were collected as frequently as every 4–6 h using a 1-m^2 EZNET (Eastern Marine Marsh), the marketed version of the BIONESS (Bedford Institute of Oceanography Net and Environmental Sampling System; Sameoto et al. 1980). The EZNET was fitted with 10 opening and closing nets and was deployed to sample 10 discrete depths. When sea state and wind conditions limited the deployment of the EZNET, a Bongo sampler (Posgay and Marak 1980) was deployed using double oblique tows between the surface and ~5 m above bottom to provide depth-integrated samples.

Upon retrieval, all net samples were examined and all cod larvae were removed and counted. When available, a minimum of 10 cod larvae from each net were videotaped for standard length estimates and other morphometric analysis and then individually preserved in liquid nitrogen. The eyeballs of the larvae were later removed and sent to the Marine Gene Probe Laboratory (MGPL) for DNA analyses. Standard length estimates determined from the videotaped images were employed to assign an age to each larva according to an age–length relationship previously established for cod larvae collected on the Scotian Shelf (M. Meekan, Université Laval, Québec, unpublished data). The larval ages were subsequently used to select a subset of individuals that, according to their lengths, would have been born within the same 5- to 6-d period near the beginning of the sampling period.

Additional details of the shipboard data collection, nowcasting system, cruise evolution, and larval collections can be found in Griffin and Lochmann (1993), Bowen et al. (1995), and Taggart et al. (1996).

DNA fingerprinting

Each larva was DNA fingerprinted with six microsatellite probes named Gmo 2, Gmo 4, Gmo 120, Gmo 132, Gmo 141, and Gmo 145. These microsatellite markers are based on dinucleotide repeats and were developed in the MGPL. Details concerning sequences and protocols of PCR amplification for several of these probes can be found in Wright (1993) and Brooker et al. (1994). The microsatellites used in the present study are hypervariable single-locus markers; each larva has two alleles, one inherited from each parent.

A total of 1359 larvae were fingerprinted. Scores were obtained from 1303 larvae for Gmo 2, 1313 larvae for Gmo 132, 1226 larvae for Gmo 120, 1289 larvae for Gmo 141, 1229 larvae for Gmo 145, and 999 larvae for Gmo 4. A total of 857 larvae were successfully scored for all six markers and represented larvae collected among sample dates, depths, and gear (Table 1). Using all of these 857 larvae to build every pairwise comparison would have yielded more than 350 000 likelihood ratios. We thus restricted the analysis to the larvae collected from the seven largest daily consecutive sampling stations before and after the storm that interrupted sampling (Table 1). Stations 57 (29 November), 59 (30 November), 72 (1 December), 81 (2 December), and 90 (3 December) were chosen as they had the largest number of completely scored larvae and represented a 5-d consecutive series of samples collected from the larval cohort prior to the storm period. Stations 123 (10 December) and 126 (11 December) had the largest number of larvae found after the storm. All larval collections from these seven stations were made using the EZNET sampler and thus included depth-structured subsamples. These seven stations had the highest daily success in terms of the number of captured larvae for a given volume of sampled water. There was thus a higher probability that the larvae from these stations had been sampled from the core of the tracked cohort. These stations were then deemed to be the most informative "representatives" of the tracked cohort.

Inferring kinship from microsatellite information

Reference frequencies and probabilities, and estimation of group relatedness

For each single-locus marker, three classes of allele-sharing states can be defined for a pair of individuals: (1) class C_0: the two individuals in the pair have no common allele for that marker (e.g. genotype AB and CD, or AB and CC), (2) class C_1: the two individuals have one common allele (e.g., genotype AB and AC, or AB and BB), and

© 1997 NRC Canada

Table 1. Stations, sampling gear, and sampling dates during the tracking cruise.

Station	Gear[b]	Date	No. of larvae[c]	Station	Gear[b]	Date	No. of larvae[c]
28	B	26 Nov.	10	82	E	2 Dec.	23
33	B	26 Nov.	3	87	E	2 Dec.	30
38	B	26 Nov.	8	88	E	2 Dec.	22
41	E	26 Nov.	14	90[a]	E	3 Dec.	26
44	E	27 Nov.	11	92	B	8 Dec.	1
45	E	27 Nov.	13	95	B	8 Dec.	2
46	B	27 Nov.	16	100	B	9 Dec.	4
54	E	28 Nov.	25	101	B	9 Dec.	6
56	E	29 Nov.	43	108	B	9 Dec.	8
57[a]	E	29 Nov.	80	109	B	9 Dec.	7
58	E	29 Nov.	44	110	B	9 Dec.	3
59[a]	E	30 Nov.	61	119	E	10 Dec.	4
60	E	30 Nov.	1	120	E	10 Dec.	3
62	E	30 Nov.	30	122	E	10 Dec.	1
67	B	1 Dec.	17	123[a]	E	10 Dec.	18
68	B	1 Dec.	1	126[a]	E	11 Dec.	26
69	B	1 Dec.	1	131	B	12 Dec.	7
71	E	1 Dec.	5	133	B	12 Dec.	5
72[a]	E	1 Dec.	71	136	B	12 Dec.	9
73	E	1 Dec.	19	137	B	12 Dec.	5
78	E	1 Dec.	54	138	B	12 Dec.	8
79	E	2 Dec.	11	139	B	14 Dec.	5
80	E	2 Dec.	25	142	B	15 Dec.	5
81[a]	E	2 Dec.	59	146	B	16 Dec.	7

[a]Chosen representative station.
[b]B = Bongo, E = EZNET.
[c]Total number of larvae for which complete scores from six markers were obtained.

(3) class C_2: the two individuals have two common alleles (e.g., AB and AB, or AA and AA).

These three classes are essentially similar to those defined by the Cotterman coefficients (Cotterman 1940, discussed in Crow and Kimura 1970; Thompson 1991). For a group of individuals, the observed frequencies of these three classes of allele sharing can be computed over all possible pairwise comparisons in the population, for each single locus marker ($Fr(C_0)$; $Fr(C_1)$; $Fr(C_2)$).

It is also possible to calculate the probabilities of observing the three classes of allele sharing (C_0, C_1, and C_2) among individuals with a specific level of relatedness, drawn from a population with the same allelic frequencies as estimated in the sample (Thompson 1991: Brookfield and Parkin 1993). In the present study, three sets of probabilities were calculated for three levels of relatedness (for individuals drawn at random in the population, which are defined to be unrelated individuals, for half-sibs, and for full-sibs): set 1: probabilities of observing C_0, C_1, and C_2 among random (unrelated) individuals drawn from a population with the same underlying allelic frequencies ($P(C_0)/R$; $P(C_1)/R$; $P(C_2)/R$), Set 2: probabilities of observing C_0, C_1, and C_2 among half-sibs drawn from a population with the same underlying allelic frequencies ($P(C_0)/H$; $P(C_1)/H$; $P(C_2)/H$),and Set 3: probabilities of observing C_0, C_1, and C_2 among full-sibs drawn from a population with the same underlying allelic frequencies ($P(C_0)/F$; $P(C_1)/F$; $P(C_2)/F$).

The observed frequencies of the three classes of allele sharing as well as the probabilities of the three classes of allele sharing were calculated for each marker using all the data in the sample (e.g., all 1313 larvae with Gmo 132 scores, all 999 larvae with Gmo 4 scores, etc.).

There are two ways in which a pair of individuals can have a common allele. They may have inherited it from a common ancestor, in which case the common allele is "identical by descent" in the two individuals. Alternatively, they may have the same allele simply by chance because there is not an infinite number of alleles in the population. The average coefficient of genetic relatedness of a group of individuals can be defined as the average percentage of genes identical by descent in that group. It can be easily shown that for unrelated individuals, the probability of having 0, 1, or 2 common alleles identical by descent should be (1, 0, 0); it should be (0.5, 0.5, 0) for half-sibs and (0.25, 0.50, 0.25) for full-sibs (Thompson 1991). In the present study, the group average relatedness of each of the seven sample collections was estimated by ($Fr(C_2) + 0.5 \cdot Fr(C_1)$), the frequencies being calculated in each of the sample collections. We used only the markers that showed sets of probabilities ($P(C_i)/R$ or H or F) close to the rate of allelic identity by descent for the three categories of relatedness, respectively.

Likelihood ratio

For a pair of individuals, the actual realized pattern of allele sharing for the six available markers is easy to observe. For example, such a pattern could be individuals X and Y have 0 alleles common for markers Gmo 2, Gmo 141, and Gmo 4, one allele common for markers Gmo 120 and Gmo 145, and two alleles common for marker Gmo 132. If the markers are located on different chromosomes and thus segregate independently, it is then easy to calculate what would be the overall probabilities of observing this particular pattern among two unrelated individuals (overall probability = R) or among half-sibs (overall Probability = H) or among full-sibs (overall probability = F) simply by multiplying the appropriate probabilities ($P(C_i)/R$, or $P(C_i)/H$ or $P(C_i)/F$) for each single locus marker. The fact that the six markers used in the study segregate independently was verified in this and several other cod populations using the

© 1997 NRC Canada

genotypic linkage disequilibrium testing capability of the GENEPOP population genetic software (available from M. Raymond and F. Rousset, Laboratoire de Génétique et Environnement, Institut des Sciences de l'Evolution, 34095 Montpellier cedex 05, France).

Two likelihood ratios can then be constructed. Likelihood (H/R) = H/R = odds of observing the pattern of allele shared if the two individuals are half-sib versus the two individuals are drawn at random from the population (unrelated). Likelihood (F/R) = F/R = odds of observing the pattern of alleles shared if the two individuals are full-sib versus the two individuals are drawn at random from the population (unrelated). High likelihood (H/R) or (F/R) thus indicates a pair of individuals with patterns of allele sharing that are more likely to be seen if two individuals are half-sib or full-sib than if they are randomly drawn (unrelated). These likelihood ratios were constructed for all pairs of larvae with complete scores within each of the seven representative sample collections (e.g., every larva from station 57 compared with every other larva from that same station). Likelihood ratios were also constructed for all pairs of larva among some collections (i.e., every larva from station 57 compared with every larva from stations 59 and 81; every larva from station 59 compared with every larva from station 81).

Significance of the likelihood ratio and estimation of individual pairwise relatedness

There are three classes of allele sharing for each locus and six loci were used in the present study. There are thus $3^6 = 729$ possible combinations of allele sharing for any pair of individuals. The two likelihood ratios F/R and H/R can be calculated for each of the 729 possible combinations. It is also possible to calculate the frequencies at which this particular combination should be observed by chance in the population simply by multiplying the six observed frequencies of allele sharing from the six markers ($\mathrm{Fr}(C_i)$). For each value of the likelihood ratio, one can therefore calculate the probability of observing a likelihood ratio as high or higher by chance alone, i.e., the significance of that likelihood ratio. This approach is essentially similar to a bootstrap approach where the scores would be randomized among the various larvae and a large number of likelihood ratios would be constructed from the permutated data to estimate the significance of the observed likelihood ratio.

With the present data, there is no extraneous information available that would allow a priori pinpointing of specific pairs of potentially related larvae among all possible pairs of larvae. Our approach is therefore to build the likelihood ratios (H/R) and (F/R) and their associated significance for every pair of larvae within the groups of interest. This generates a large number of likelihood ratios, of which some will appear highly significant by chance alone.

Consider a group of 100 unrelated larvae. A total 4950 likelihood ratios (H/R) or (F/R) can be constructed from every pairwise comparison. One can expect 247.5 ratios (5% of 4950) to have a 5% significance level, 49.5 ratios (1% of 4500) to have a 1% significance level, and so on. In this study, the potential presence of relatedness in the group was analyzed by comparing the number of ratios found to be significant at 5 and 1% with what could be expected by chance alone, and testing whether departures from expectations were statistically significant. The significance of individual pairwise likelihood ratios was also tested using the Bonferroni approximation, i.e., in our example, to test at 5%, a likelihood ratio should be significant at 0.05/4950 = 0.00001.

Results

Overall relatedness within groups

All six markers are hypervariable with 29–63 alleles observed per locus in the sample (Table 2). For every marker and every class of allele sharing, there is a close fit between the observed frequency ($\mathrm{Fr}(C_i)$) and the probability among unrelated individuals in a population with the same underlying allelic frequencies ($P(C_i)/R$) (Table 2). This indicates that most pairs of larvae in the sample are behaving as if their alleles were drawn at random in the gene pool (i.e., most pairs appear unrelated).

The four most variable markers, Gmo 120, 141, 145, and 4, appear suitable to estimate the average coefficient of genetic relatedness as outlined in the Material and methods section. The calculated $P(C_0)/R$; $P(C_1)/R$ and $P(C_2)/R$ probabilities for Gmo 120, 141, 145, and 4 are not very far from the expected rate of allelic identity by descent (1, 0, 0) for unrelated individuals (Table 2). Similarly, the probabilities among half-sibs and full-sibs are not very far from the expected ((0.5, 0.5, 0.0) and (0.25, 0.50, 0.25)), respectively (Table 2).

With each of the four markers, the average genetic relatedness as estimated by $(\mathrm{Fr}(C_2) + 0.5 \cdot \mathrm{Fr}(C_1))$ will be slightly overestimated (particularly for unrelated individuals) compared with the true values that would be obtained if the markers would only detect identity by descent. The average overestimation for the three classes of relatedness (random/unrelated, half-sib, full-sib) can be calculated simply by substituting $\mathrm{Fr}(C_1)$ and $\mathrm{Fr}(C_2)$ by $P(C_1)/R$ and $P(C_2)/R$ or by $P(C_1)/H$ and $P(C_2)/H$ or by $P(C_1)/F$ and $P(C_2)/F$, respectively, in the equation: average genetic relatedness = $(\mathrm{Fr}(C_2) + 0.5 \cdot \mathrm{Fr}(C_1))$. The four markers will overestimate by 0.025–0.04 the true average genetic relatedness of full-sibs (0.5), by 0.035–0.06 the true average genetic relatedness of half-sibs (0.25), and by 0.066–0.11 the true average genetic relatedness of unrelated individuals (0.0) (Table 3, upper portion).

With each of the four markers, the estimated average genetic relatedness levels among the larvae from the seven sample collections are essentially the levels that would be expected among individuals drawn at random (unrelated) (Table 3, lower portion). There was thus no indication that any of the groups of larvae from the cohort sampled at different times were groups of related larvae.

Likelihood ratios and individual relatedness

Likelihood ratios and their significance were constructed for every pair of larvae within each of the seven sample collections, as well as across some stations (57 and 59; 57 and 81; 59 and 81). Examining the distribution of likelihood ratios to look at individual pairwise relatedness is more sensitive to the existence of family structure than the overall calculation of relatedness within groups as given above.

No pairs of larvae were found with a significant level of relatedness using the Bonferroni adjusted significance levels.

There was no significant difference between the number of likelihood ratios (H/R) and (F/R) significant at 5 and 1% and what could be expected by chance alone, both within and among sample collections (Table 4 illustrates this with the comparisons within station 81 and across stations 57 and 59). There was no evidence of finding more sibling relationship within sample collections than across collections. Similarly, there was no apparent change with time (in successive station collections) or in association with the passage of a storm during the sampling cruise. In every instance, the numbers of likelihood ratios (H/R) and (F/R) significant at 5 and 1% matched fairly closely what could be expected by chance alone among individuals drawn at random (unrelated). No significant deviation was observed in any of these comparisons.

© 1997 NRC Canada

Table 2. Observed frequencies and calculated probabilities of observing C_0, C_1, and C_2 classes of allele sharing in the sample.

Marker	No. of larvae analyzed	No. of alleles observed	Class of allele sharing	Observed frequency Fr(C_i)	Probability among random fish $P(C_i)/R$	Probability among half-sibs $P(C_i)/H$	Probability among full-sibs $P(C_i)/F$
Gmo 2	1303	29	C_0	0.443	0.436	0.218	0.109
			C_1	0.492	0.497	0.645	0.521
			C_2	0.066	0.067	0.137	0.370
Gmo 132	1313	31	C_0	0.458	0.450	0.225	0.113
			C_1	0.477	0.488	0.643	0.521
			C_2	0.065	0.062	0.132	0.367
Gmo 120	1226	43	C_0	0.819	0.823	0.411	0.206
			C_1	0.176	0.173	0.562	0.519
			C_2	0.005	0.005	0.026	0.275
Gmo 141	1289	63	C_0	0.888	0.885	0.443	0.221
			C_1	0.110	0.113	0.542	0.513
			C_2	0.002	0.002	0.016	0.266
Gmo 145	1229	48	C_0	0.790	0.792	0.396	0.198
			C_1	0.203	0.202	0.572	0.522
			C_2	0.007	0.006	0.032	0.281
Gmo 4	999	62	C_0	0.847	0.849	0.424	0.212
			C_1	0.150	0.148	0.554	0.517
			C_2	0.004	0.003	0.022	0.271

Table 3. Estimation of average genetic relatedness among the larvae from seven representative sampling stations.

Estimated average genetic relatedness	Gmo 120	Gmo 141	Gmo 145	Gmo 4
Among unrelated fish	0.090	0.060	0.110	0.075
Among half-sibs	0.305	0.285	0.310	0.300
Among full-sibs	0.535	0.525	0.540	0.530
Within station 57	0.105	0.060	0.120	0.085
Within station 59	0.115	0.060	0.105	0.080
Within station 72	0.105	0.060	0.105	0.080
Within station 81	0.080	0.060	0.080	0.085
Within station 90	0.075	0.075	0.095	0.085
Within station 123	0.120	0.065	0.135	0.065
Within station 126	0.090	0.055	0.115	0.090

The same result was obtained when the analysis was restricted to the subset of larvae estimated to have been born during the same 5- to 6-d time window ("same-day" larvae) (Table 5). For example, the number of significant likelihood ratios (*H/R*) and (*F/R*) at 5 and 1% among the 32 "same-day" larvae from station 59 and the 27 "same-day" larvae from station 72 was not significantly different from what could be expected by chance alone (Table 5).

Within stations, there was no evidence of a spatial family structure among and across samples collected by individual nets at various depths (Table 6). Within station 81 for example, the 74 and 87 pairs found with 5% level likelihood ratios (*H/R*) and (*F/R*), respectively (Table 4), were as often found among the same nets as across nearby nets or across more distant nets (Table 6).

Discussion

The null hypothesis in this study is that none of the larvae sampled are half- or full-sib (i.e., that they have no common parents, they are unrelated at the first generation level), while the alternative hypothesis is that at least some of the individuals are siblings. Of course, it is possible that some of the pairs of larvae that exhibited high likelihood ratios in this study were indeed true full- or half-sib, but overall we could not reject the null hypothesis that the occurrence of every pair of larvae with high likelihood ratios observed in this study could be explained by chance alone.

Ultimately, the power of such an approach to detect family structure rests, on one hand, with the number of independently segregating markers that can be used and with the informativeness (i.e., allelic variability) of these markers and, on the other hand, with the actual level of family structure in the sample. If the tested population has a high level of family structure and consists of a collection of half- and full-sibs (a fairly extreme form of the alternative hypothesis), the method described here will generally be powerful at detecting that there are more high likelihood ratios than what can be explained by chance alone. For example, this approach has been used in salmonid aquaculture populations with known family structure and has proven successful at identifying siblings versus more distantly related individuals (Doyle et al.

© 1997 NRC Canada

Table 4. Expected and observed numbers of significant likelihood ratios (*H*/*R*) and (*F*/*R*) within station 81 and across stations 57 and 59.

	Within station 81	Across stations 57 and 59
No. of pairwise comparisons	1711	4880
No. of observed likelihood ratios (*H*/*R*) at 5%	74	231
No. of observed likelihood ratios (*F*/*R*) at 5%	87	245
Expected no. of likelihood ratios significant at 5% by chance alone	85	244
No. of observed likelihood ratios (*H*/*R*) at 1%	17	46
No. of observed likelihood ratios (*F*/*R*) at 1%	20	52
Expected no. of likelihood ratios significant at 1% by chance alone	17	49

Table 5. Expected and observed numbers of significant likelihood ratios (*H*/*R*) and (*F*/*R*) within "same-day" larvae from stations 59 and 72.

	Within "same-day" larvae, station 59	Within "same-day" larvae, station 72
No. of pairwise comparisons	496	351
No. of observed likelihood ratios (*H*/*R*) at 5%	19	16
No. of observed likelihood ratios (*F*/*R*) at 5%	22	14
Expected no. of likehood ratios significant at 5% by chance alone	25	17.5
No. of observed likelihood ratios (*H*/*R*) at 1%	2	2
No. of observed likelihood ratios (*F*/*R*) at 1%	4	2
Expected no. of likelihood ratios significant at 1% by chance alone	5	3.5

1995). In a recent double-blind experiment, 57 of 60 California chinook salmon (*Oncorhynchus tshawytscha*) were correctly classified as full-sib, half-sib, or unrelated using six markers considerably less informative (four alleles per loci in average) than the ones used here (D. Hedgecock, University of California at Davis, Davis, Calif., personal communication). If, however, the tested population should consist mostly of unrelated individuals but include a few siblings (a more subtle form of the alternative hypothesis), the approach described here will not easily distinguish the few true siblings from pairs of individuals that exhibit similar DNA fingerprint by chance alone. However, the true siblings will exhibit increasing likelihood ratios, while the false ones will exhibit decreasing ratios as additional DNA markers are used. Ultimately, when enough markers are used, the true siblings (however few) will stand out and will exhibit significant Bonferroni-adjusted likelihood ratios. That has not happened in the present study.

The family structure of a natural assemblage of larvae or juveniles from most marine animals, including cod, is largely unknown. Large interannual variation in cod recruitment is consistent with the notion that some spawning aggregations may be small. Female cod are known to be multiple-batch spawners characterized by high fecundity (Kjesbu and Holm 1994). Although juvenile and adult cod are widely distributed, spawning is known to occur at certain regular times and restricted locations where large numbers of putative spawners aggregate (Brander 1994). Brawn (1961) observed, pair matings in cod maintained in aquaria. Some aggressive males were able to establish territories and generally one dominant male monopolized most of the reproductive activity. However, female cod were also seen to spawn without the direct presence of males (broadcast spawning) on a few occasions (Brawn 1961). Actual mating behaviour of cod in the spawning aggregations cannot easily be observed and the extent to which broadcast spawning and/or pair matings and/or dominance by some males occurs in large cod aggregations in nature is still largely unknown. A cohort of larvae may represent a very large number of parents if broadcast spawning takes place. Alternatively, if cohorts are derived predominantly from single batches of spawn from several females with pair matings, cohorts would then represent a mixture of relatively few full-sib families. If, in addition, some males dominate the reproductive activity, cohorts may comprise relatively few paternal half-sib families.

It is likely that this cohort of cod larvae was a fairly homo-

© 1997 NRC Canada

Table 6. Expected and observed number of significant likelihood ratios (*H*/*R*) and (*F*/*R*) among and across the various nets of station 81.

Distance between nets[a]	No. of pairwise comparisons within station 81	No. of likelihood ratios (*H*/*R*) at 5%	Expected distribution of 74 cases among nets	No. of likelihood ratios (*F*/*R*) at 5%	Expected distribution of 87 cases among nets
0	236	15	10.2	14	12
1	385	15	16.6	18	19.6
2	355	15	15.3	22	18.1
3	285	12	12.3	14	14.5
4	212	8	9.2	9	10.8
5	128	3	5.5	5	6.5
6	110	6	4.8	5	5.6
Total	1711	74	74	87	87
		$\chi^2 = 4.00$ (NS)		$\chi^2 = 2.04$ (NS)	

[a]0 means larvae from same net, 1 means larvae from one net apart, etc.

geneous mixture of larvae that were not half- or full-sib. No larval pairs could be conclusively shown to have common parents (i.e., by having exceptionally high levels of allele sharing, relative to expectations from randomly drawn larval pairs). This cohort probably did not originate from a small number of pair matings, and no evidence of male dominance on the reproductive activity could be found. It appears more likely that this cohort originated from unpaired matings (broadcast spawning) of a parental population that was at least twice as large (males + females) as the number of larvae analyzed.

However, one cannot completely disregard the possibility that the absence of family structure in this cohort simply reflected considerable oceanic mixing occurring immediately after spawning. Yet the larvae were still very young (5–9 d old) at the time of the first analyzed sampling (station 57), and the ship "nowcasting system" appears to have convincingly tracked the same water mass over the cruise period (Bowen et al. 1995).

Assuming that the larvae analyzed in detail here (315 individuals from the seven collections) were indeed representative of the 1400 or so larvae collected and fingerprinted in the present study, we can estimate that a minimum of 1400 parent cod of each sex (i.e., 2800 parent cod in total) contributed to this cohort, since no two larvae appeared to have common parents. This "minimum parental population", inferred from the observation that the larvae are not siblings and each has two parents, is equivalent to a lower bound on the inbreeding effective population size, Ne, defined as $Ne = 4 \cdot Nf \cdot Nm/(Nf + Nm)$ Hartl and Clark 1989, p. 86). This is, to our knowledge, the first time that a lower bound estimate of effective population size in a naturally mating cod population has been obtained, without requiring extraneous assumptions about genetic marker mutation rates. The actual number of individual parents present in the spawning aggregation would be larger than this estimate, particularly if there is large parental variation in fecundity and offspring survival.

The second goal of this study was to see if the action of natural selection among sibship could be directly observed. This could not be done in the present study, since the presence of sibship was not detected. No first-generation family structure was detected, and thus, family-specific mortality could not be observed, even if it did happen in this cohort as it had in laboratory-reared cod larvae (Doyle et al. 1995).

Acknowledgments

This research was supported by the Ocean Production Enhancement Network (OPEN), one of the 15 Networks of Centres of Excellence supported by the Government of Canada from 1990 to 1994, and designed to pursue collaborative research in a strategic area of national importance. OPEN's research focused primarily on fisheries oceanography. Much of the success of the tracking cruise relied on the shelf circulation model developed by D.A. Griffin and K.R. Thompson. G.L. Maillet managed the larvae collection and extracted the larvae eyeballs for the DNA analyses which were performed in part by L. Atkinson and D. Parmentier.

References

Bowen, A.J., Griffin, D.A., Hazen, D.G., Matheson, S.A., and Thompson, K.R. 1995. Shipboard nowcasting of shelf circulation. Continental. Shelf Res. **15**: 115–128.

Brander, K.M. 1994. Patterns of distribution, spawning, and growth in North Atlantic cod: the utility of inter-regional comparisons. ICES Mar. Sci. Symp. **198**: 406–413.

Brawn, V.M. 1961. Reproductive behaviour of the cod (*Gadus Callarias* L.). Behaviour, **18**: 177–198.

Brooker, A.L., Cook, D., Bentzen, P., Wright, J.M., and Doyle, R.W. 1994. Organization of microsatellites differs between mammals and teleost fishes. Can. J. Fish. Aquat. Sci. **51**: 1959–1966.

Brookfield, J.F.Y., and Parkin, D.T. 1993. Use of single-locus DNA probes in the establishment of relatedness in wild populations. Heredity, **70**: 660–663.

Cotterman, C.W. 1940. A calculus for statistico-genetics. Ph.D. thesis, Ohio State University. *In* Genetics and social structure. Benchmark papers in genetics. *Edited by* P. Ballonoff. Dowden, Hutchinson & Ross, Inc., Stroudsburg, Pa. pp. 1975. 157–272.

Crow, J.F., and Kimura, M. 1970. An introduction to population genetics theory. Harper and Row, New York. pp. 132–136.

© 1997 NRC Canada

Doyle, R.W., Herbinger, C.M., Taggart, C.T., and Lochmann, S.E. 1995. Use of DNA microsatellite polymorphism to analyze genetic correlations between hatchery and natural fitness. Am. Fish. Soc. Symp. **15**: 205–211.

Griffin, D.A., and Lochmann, S.E. 1993. *Petrel V* cruise 31 to Western bank, 22 November – 16 December 1992. OPEN Rep. 1993/1, Department of Oceanography, Dalhousie University, Halifax, N.S.

Hartl, D.L., and Clark, A.G. 1989. Principles of population genetics. 2nd ed. Sinauer Associates, Inc., Sunderland, Mass.

Hedgecock, D. 1994*a*. Does variance in reproductive success limit population sizes of marine organisms? *In* Genetics and evolution of aquatic organisms. *Edited by* A.R. Beaumont. Chapman and Hall, London. pp. 122–134.

Hedgecock, D. 1994*b*. Population genetics in marine organisms. U.S. Globec News, **6**: 7–11.

Kjesbu, O.S., and Holm, J.C. 1994. Oocyte recruitment in first-time spawning Atlantic cod (*Gadus morhua*) in relation to feeding regime. Can. J. Fish. Aquat. Sci. **51**: 1893–1898.

Lambert, T.C. 1984. Larval cohort succession in herring (*Clupea harengus*) and capelin (*Mallotus villosus*). Can. J. Fish. Aquat. Sci. **41**: 1552–1564.

Lynch, M. 1988. Estimation of relatedness by DNA fingerprinting. Mol. Biol. Evol. **5**: 584–599.

Posgay, J.A., and Marak, R.R. 1980. The MARMAP bongo zooplankton samplers. J. Northwest Atl. Fish. Sci. **45**: 91–99.

Sameoto, D.D., Jarosynski, L.O., and Fraser, W.B. 1980. The BIONESS — new design in multiple net zooplankton samplers. J. Fish. Res. Board Can. **37**: 722–724.

Taggart, C.T., and Frank, K.T. 1990. Perspectives on larval fish ecology and recruitment processes. Probing the scales of relationships. *In* Large marine ecosystems: patterns, processes, and yields. *Edited by* K. Sherman, L.M. Alexander and B.D. Gold. AAAS Selected Symposium Series. pp. 151–164.

Taggart, C.T., Thompson, K.T., Mailler, G.L., Lochmann, S.E., and Griffin, D.A. 1996. Abundance distribution of larval cod (*Gadus morhua*) and zooplankton in a gyre-like water mass on the Scotian Shelf. *In* Survival strategies in early life stages of marine resources. Proc. Int. Workshop, Yokohama. *Edited by* Y. Watanabe, Y. Yamashita, and Y. Oozeki. Balkema Press, Rotterdam, The Netherlands. pp. 155–173.

Thompson, E.A. 1991. Estimation of relationships from genetic data. *In* Handbook of statistics. Vol. 8. *Edited by* C.R. Rao and R. Chakraborty. Elsevier, Amsterdam, The Netherlands. pp. 255–269.

Wetton, J.H., Carter, R.E., Parkin, D.T., and Walters, D. 1987. Demographic study of a wild house sparrow population by DNA fingerprinting. Nature (Lond.), **327**: 147–149.

Wright, J.M. 1993. DNA fingerprinting of fishes. *In* Biochemistry and molecular biology of fishes. Vol. 2. *Edited by* P.W. Hochachka and T. Mommsen. Elsevier, Amsterdam, The Netherlands. pp. 57–91.

Wright, J.M., and Bentzen, P. 1994. Microsatellites: genetic markers for the future. Rev. Fish Biol. Fish. **4**: 384–388.

© 1997 NRC Canada

Protracted spawning of Atlantic cod (*Gadus morhua*) in Newfoundland waters: evidence from otolith microstructure

David L. Pinsent and David A. Methven

Abstract: The most common method used to estimate the time of Atlantic cod (*Gadus morhua*) spawning in Newfoundland waters has been to examine the reproductive condition of the adult gonad. As an alternative method, we aged small juvenile cod (<60 mm SL) using lapillus otolith microstructure and backcalculated the spawning date of each individual. Juveniles collected in the shallow coastal waters of Trinity Bay from May 1993 to January 1994 revealed a highly protracted spawning period in 1993. The duration of backcalculated spawning dates in 1993 was almost 12 wk longer than any range previously reported from the Newfoundland region. We suggest that juvenile cod collected inshore, in southern Trinity Bay, originate from a combination of both inshore and offshore spawning events.

Résumé : La méthode la plus couramment employée pour estimer les dates de la fraye de la morue franche (*Gadus morhua*) dans les eaux de Terre-Neuve consiste à déterminer la condition génésique des gonades chez les adultes. Comme autre méthode, nous avons eu recours à la détermination de l'âge de petites morues juvéniles (<60 mm LS) en utilisant la microstructure des lapillus (otolithes), et déduit la date de la ponte dont chaque individu était issu. Les juvéniles prélevés dans des eaux côtières peu profondes de mai 1993 à janvier 1994 ont permis de conclure que la période de fraye de 1993 avait été grandement prolongée. La fourchette des dates de fraye déduites par cette méthode était plus étendue que celle signalée jusque-là pour la morue dans la région de Terre-Neuve, et ce, d'environ 6 sem aux deux extrémités de la fourchette. Nous avançons l'explication que les morues juvéniles prélevées sur la côte, dans le sud de la baie de la Trinité, sont le produit d'épisodes de ponte ayant eu lieu dans les eaux à la fois côtières et hauturières.
[Traduit par la Rédaction]

Introduction

The high fecundity of many teleosts is one of several adaptations that ensures the maintenance of local populations (Svardson 1949) under conditions of extreme egg and larval mortality (Cushing 1981; Hunter 1981; Pepin 1991). Within the Gadidae, high fecundity is characterized by the production of many buoyant eggs (Wenner 1983; Dunn and Matarese 1984) that are broadcast into prevailing currents enabling species to exploit downstream juvenile nursery areas (Harden Jones 1968; Suthers et al. 1989). Spawning times and, presumably, spawning migrations may have evolved to provide optimum conditions for newly spawned eggs and larvae (Scott 1979; Cushing 1990; Brander and Hurley 1992).

In the Newfoundland region, the spawning times and locations of Atlantic cod (*Gadus morhua*) appear to be somewhat protracted (Myers et al. 1993) and widespread (Hutchings et al. 1993), suggesting that adequate conditions for eggs and larvae vary in space and time. Spawning is reported to begin in March and continue into early April off Labrador and occurs mainly during April and May on the banks and slope of the northeast Newfoundland Shelf (Templeman 1981; Myers et al. 1993). Spawning on the northern Grand Bank (NAFO Division 3L) was reported by Templeman (1981) to range from April to June, and Myers et al. (1993) calculated 9 June as the mean spawning date for 3L. The documented range of spawning times for coastal regions of Newfoundland is also quite protracted (Thompson 1943). There are reports of hydrated eggs (likely to be released within 3 d) or actively spawning females along the coast from April until September, but inshore spawning is concentrated in May and June (Hutchings et al. 1993; Smedbol and Wroblewski 1997). Each of these works has determined cod spawning times from the reproductive condition of adult gonad.

The documented duration of cod spawning in the Newfoundland region has been assumed to produce a single cohort of juveniles that settle in coastal and offshore nursery areas in autumn (Serebryakov 1968; Lear and Green 1984; Lear and Wells 1984). However, the possibility of a more protracted spawning season has been indicated by the presence of recently settled juvenile cod (<60 mm standard length (SL)) inshore from April to June and from August to November (Methven and Bajdik 1994). We examine whether newly settled cod collected throughout the year originate from a single spawning event or if there is evidence for spawning throughout much of the year. This is addressed by using lapillus otolith microstructure to backcalculate hatching and spawning dates.

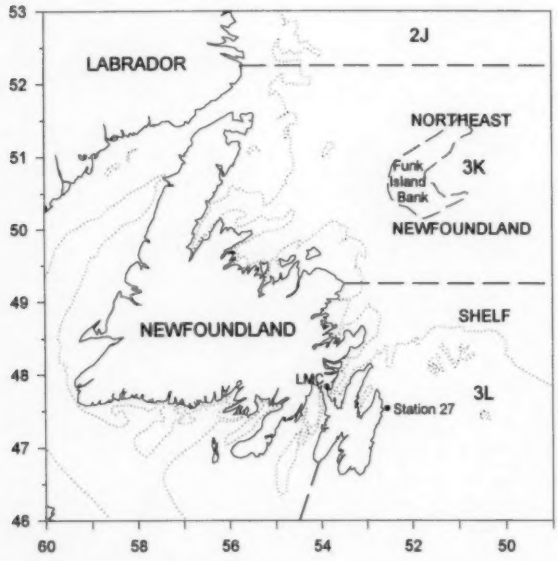
Received February 17, 1995. Accepted March 29, 1996.
J13447

D.L. Pinsent[1] and D.A. Methven. Ocean Sciences Centre and Department of Biology, Memorial University of Newfoundland, St. John's, NF A1B 3X9, Canada.

[1] Present address: Jacques Whitford Environment Limited, 607 Torbay Rd., St. John's, NF A1A 4Y6, Canada.

© 1997 NRC Canada

Fig. 1. Map of Newfoundland showing the location of Little Mosquito Cove (LMC) sampling site in southern Trinity Bay, hydrographic station 27, NAFO Divisions 2J, 3K, and 3L, and Funk Island Bank.



Materials and methods

Sampling site, methods, and gear

The sampling site, Little Mosquito Cove (Fig. 1; 47°50.5′N, 53°53.9′W), is a sheltered shallow (predominately <10 m) estuarine cove located in Bull Arm, southwestern Trinity Bay, Newfoundland. The bottom nearshore consists of small rocks covered by a thin layer of silt. A few metres offshore, the bottom changes to mud, supporting dense beds of eel grass (*Zostera marina*). Eel grass does not occur on the muddy bottom at depths >5 m.

Juvenile cod were collected at approximately 2-wk intervals from late May 1993 to early January 1994. All collections were made during the day, within an hour of low tide, using a 25-m beach seine with a 9-mm stretch mesh liner (see Schneider et al. 1997). The seine was deployed by boat to a distance of 55 m offshore and retrieved by two individuals standing 16 m apart on shore. The seine sampled from the substrate to about 2 m above the bottom.

Biological data collection

Juvenile Atlantic cod were identified and separated from cooccurring Greenland cod (*Gadus ogac*) and other bycatch, labelled, and frozen within 2–4 h of collection. Cod were measured for SL to the nearest millimetre after being thawed in the laboratory. Small juveniles (<60 mm SL) were selected for age determination from four times of the year: early January, just prior to the formation of landfast ice; May–June, after departure of landfast ice; and during mid-August and November. Specific sampling dates and numbers of cod aged and measured from each collection are given in Table 1.

Each cod was aged using standard lapillus otolith microstructure techniques (Stevenson and Campana 1992). Lapilli were extracted from recently thawed fish and mounted on glass slides using Crystal-Bond™. To expose the daily increments within the otolith, the lateral surface was ground to the midplane using 3-μm lapping film. Once the otolith nucleus was visible at 450× magnification, the surface was polished with 0.3-μm lapping film, making the increments around the primordia more discernable. Discontinuous increments on each lapillus were then counted at least three times at 1000× magnification. If increment counts differed by more than 10% for the same otolith, the otolith was discarded. A hand-held counter was used to eliminate any possible bias between sequential counts of the same otolith.

Daily growth increments in larval and postlarval cod otoliths have been validated as accurate and precise indicators of age in many studies (Radtke and Waiwood 1980; Bergstad 1984; Dale 1984; Campana and Neilson 1985; Campana 1989). However, there has been no validation of daily increment formation in the otoliths of cod from Newfoundland waters. To validate daily increment formation of regional juveniles, we counted the lapillus otolith increments of known-age fish, obtained from a local brood stock. From the day of hatch, five larvae were aged every 3 d for 18 d. A line representing a one-to-one match (i.e., slope = 1) of age and increment count was not significantly different (t-test, $p > 0.05$) from the linear regression of age and increment count (see Pinsent 1994).

A possible inaccuracy in otolith increment counting is the potential discrepancy between otolith readers. To measure the degree of reader bias, a random subsample ($n = 23$) of otoliths was recounted by an experienced and independent reader. We found no significant difference in the increment counts of the first and second readers (t-test, $p > 0.05$). Another potential inaccuracy in otolith reading comes from the uncertainty of whether the increments are true daily increments and not subdaily or false daily increments (Campana 1992). This is of particular concern in the outer portion of the cod lapilli, which often exhibits discontinuous increments that are much wider than increments around the nucleus. However, electron micrographs of increments in the otolith's outer margin allowed us to clearly observe an increment pattern that was consistent with adjacent increments, indicating true daily increments in the outer margin (see Pinsent 1994).

Hatch date was determined by subtracting the number of posthatch increments from the date of collection. Spawning date was calculated by subtracting the incubation period from the hatching date. To calculate the number of days required for incubation, we chose the following formula from Pepin et al. (1997):

$$(1) \quad T_{\text{hatch}} = 46.1e^{-0.17T}$$

where T_{hatch} is the number of days required to hatch at water temperature T (degrees Celsius). Water temperatures at station 27 (10 m) were selected for the model. Station 27 is located 4 km east of St. John's and is reported to be a good indicator of water temperatures along the northeast Newfoundland Shelf (Petrie et al. 1992).

Results

Throughout the year, small juvenile cod (35–60 mm SL) were selected from each collection to determine if this size class was of similar age structure. In fact, 90% of the cod selected from May to January ranged between 70 and 90 d old posthatch. The mean age and SL's of the fish aged from each collection are listed in Table 1.

Twice monthly sampling from May to January revealed the presence of cod <60 mm throughout most of the sampling period at Little Mosquito Cove. However, cod <60 mm were conspicuously absent from our collections during July and early August. This approximate 6-wk absence created two distinct cohorts of small juveniles in 1993 (Fig. 2*a*). The first cohort was already present when our sampling began in May, but consisted of few individuals <60 mm SL. A second influx of small cod into Little Mosquito Cove began in mid-August.

The hatching and spawning distributions derived from each collection suggest a highly protracted spawning and recruitment period for cod. Cod aged from the 27 May and 22 June

© 1997 NRC Canada

Table 1. Summary statistics on the length and age of cod from each collection.

Collection date	*n*	Length (mm SL)			Age (d)		
		Mean	SE	Range	Mean	SE	Range
1 Jan. 1994	10	46.6	1.8	35.9–52.8	89.5	1.49	81–94
27 May 1993	23	53.3	0.6	44.1–57.7	76.3	0.97	67–84
22 June 1993	11	52.9	1.2	44.2–56.5	80.4	1.49	72–89
26 Aug. 1993	10	42.6	1.1	39.1–50.1	77.7	1.76	71–91
16 Nov. 1993	25	53.0	0.8	45.1–59.5	79.7	1.17	67–91
30 Nov. 1993	14	53.3	1.1	44.2–60.3	81.9	2.62	71–103

collections were determined to have hatched from early March to mid-April and calculated to have been spawned from mid-January to late February (Fig. 2). Since cod <60 mm were absent in July and early August, the next fish to be aged came from the 26 August collection. These young juveniles were hatched from late May to mid-June and estimated to have been spawned from late April to late May. Cod aged from the November and January collections formed a continuous hatch date distribution from late August to late October and were calculated to have been spawned from mid-August to early October (Fig. 2). The relatively short incubation period (8–12 d) of these late summer to early autumn recruits is the result of warm water during this period.

Discussion

As determined by otolith microstructure, cod seemed to have spawned almost year-round in 1993. Spawning dates ranged from mid-January to mid-October, which extends the range of previously reported spawning times (Templeman 1981; Myers et al. 1993) by about 6 wk on each end. Protracted spawning is not an exclusive strategy to cod in the Newfoundland region. Cod on Georges Bank spawn nearly year-round, with peak spawning from January to April (Colton 1978); also, spring and autumn spawning has been observed on the Scotian Shelf (Frank et al. 1994).

Spawning events on the offshore portions of the northeast Newfoundland Shelf and slope do not usually contribute significant numbers of eggs or larvae to the bays of Newfoundland (Helbig et al. 1992; Davidson and deYoung 1995; Anderson et al. 1995). However, the outer shelf and slope regions must be regarded as possible sources of new recruits to Trinity Bay, since the only record of winter spawning in Newfoundland waters is from these offshore areas (Templeman 1981; Myers et al. 1993). A mean spawning date of 28 January was calculated for cod collected in May–June.

Small juvenile cod collected at the end of August were estimated to have been spawned in late May. These cod likely originate from within Trinity Bay because spawning inside the bay is known to peak in May–June (Hutchings et al. 1993; Smedbol and Wroblewski 1997). As coastal sampling continues into the autumn, speculation as to where these cod were spawned is more difficult. A cod <60 mm, collected in September, was likely spawned in June. Trinity Bay is still a possible source of these cod, but June is also the month of peak spawning in 3L further offshore (Myers et al. 1993). Also, most of June is within 1 standard deviation of the mean spawning date for Funk Island Bank, as reported by Myers et al. (1993). Autumn collections, then, may be a combination of juveniles from Trinity Bay as well as the northeast Newfoundland Shelf, assuming that conditions were suitable for advection to inshore areas (Helbig et al. 1992; Davidson and deYoung 1995). Finally, our late autumn and early winter collections are more likely to have been spawned within Trinity Bay because there is no record of autumn spawning on the northeast Newfoundland Shelf and slope.

Hatching and spawning date distributions backcalculated from a single collection are at risk of being biased by size- or age-selective mortality during the larval and early juvenile stages (Campana and Jones 1992). However, because mortality rate decreases with age (Peterson and Wroblewski 1984; Pepin 1989), the effect of selective mortality on backcalculated spawning dates also decreases with age. The youngest fish aged from our collections was 70 d posthatch. Consequently, the effect of selective mortality on our backcalculated hatch date distributions has been greatly decreased. The histograms presented in Fig. 2 are therefore representative of the hatching and spawning distributions for the smallest individuals in each collection.

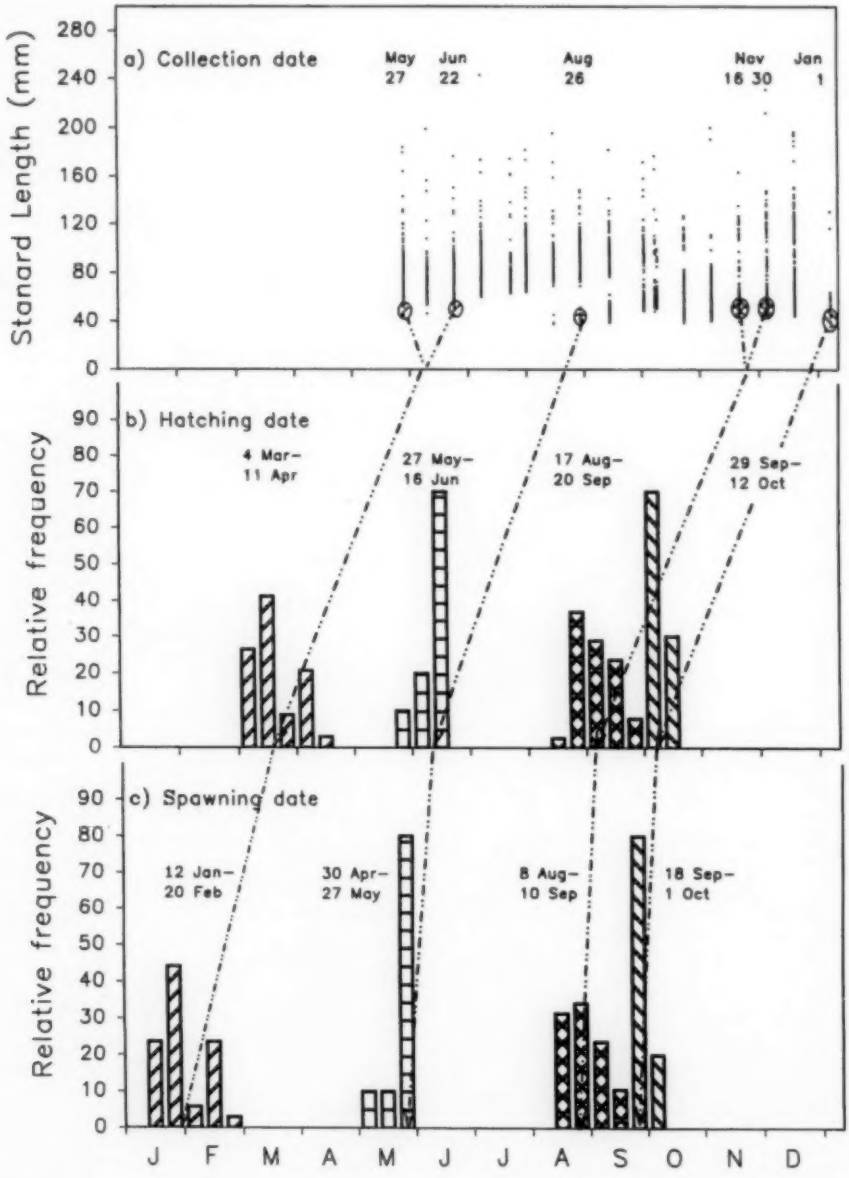
Our hatching and spawning histograms are not intended to represent the full temporal range of either event. In fact, by ageing the smaller (presumably younger) fish, we have only identified the later portion of each collection's spawning and hatching range. The larger (presumably older) fish from each collection would have hatching and spawning dates before those presented in Fig. 2. Therefore, if each spawning distribution was extrapolated to the left to represent the larger fish in each collection, cod spawning in 1993 would be near year-round.

The enigma of having cod spawn near year-round in Newfoundland waters is that shelf waters from January to April are below 1°C in the upper 30 m. These are presumably unfavourable conditions for the survival and growth of cod eggs and larvae. However, cod eggs and larvae do survive at low salinities (Yin and Blaxter 1987) and low temperatures (Laurence and Rogers 1976; Pepin et al. 1997). The fact that juveniles were collected at low temperatures (minimum value 0.4°C) and salinities (minimum value 29 ppt) during this study indicates their tolerance to relatively extreme environmental conditions. Furthermore, 0-group cod not only survive at temperatures below 1°C, they continue to grow (Brown et al. 1989).

We have demonstrated that otolith microstructure can be a valuable tool in estimating the spawning time of cod. This

© 1997 NRC Canada

Fig. 2. (*a*) Size range of cod collected at Little Mosquito Cove from 27 May to 1 January. Ellipses represent the size range of cod that were aged. Backcalculated (*b*) hatching and (*c*) spawning dates from each collection are presented at 10-d intervals. The ranges of hatching and spawning dates are indicated for each collection.



method complements the use of egg surveys (Anderson et al. 1995) and examination of adult gonads (Hutchings et al. 1993) because it calculates the spawning dates of larvae that have survived past metamorphosis. Together, these methods augment one another and decrease the uncertainty associated with any single technique.

Acknowledgements

This study was supported by the Northern Cod Science Program, Department of Fisheries and Oceans (DFO, St. John's, Nfld.). We thank D.W. Ings, K. Abbott, and L. Bussey for help with collecting and processing the fish. We appreciate the cooperation of Cynthia Mercer (DFO, St. John's) in the otolith reader validation study. Felix McCarthy of Bellevue contributed to the study with his knowledge of the local area and willingness to help overcome sampling difficulties throughout the project. The manuscript was improved thanks to the helpful comments of P. Pepin (DFO, St. John's), Jennifer Robinson, and two anonymous reviewers.

© 1997 NRC Canada

References

Anderson, J.T., Dalley, E.L., and Carscadden, J.E. 1995. Abundance and distribution of pelagic 0-group cod (*Gadus morhua*) in Newfoundland waters: inshore versus offshore. Can. J. Fish. Aquat. Sci. **52**: 115–125.

Bergstad, O.A. 1984. A relationship between the number of increments on the otoliths and age of larval and juvenile cod, *Gadus morhua*. *In* The propagation of cod *Gadus morhua* L. Proceedings of an International Symposium, Arendal, Norway 1983. *Edited by* E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Institute of Marine Research, Flødevigan Biological Station, Arendal, Norway. pp. 251–272.

Brander, K., and Hurley, P. 1992. Distribution of early-stage cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*) and witch flounder (*Glyptocephalus cynoglossus*) eggs on the Scotian Shelf: a reappraisal of evidence on the coupling of cod spawning and plankton production. Can. J. Fish. Aquat. Sci. **49**: 238–251.

Brown, J.A., Pepin, P., Methven, D.A., and Somerton, D.C. 1989. The feeding, growth and behaviour of juvenile cod, *Gadus morhua* L., in cold environments. J. Fish Biol. **35**: 373–380.

Campana, S.E. 1989. Otolith microstructure of three larval gadids in the Gulf of Maine with inferences on early life history. Can. J. Zool. **67**: 1401–1410.

Campana, S.E. 1992. Measurement and interpretation of the microstructure of fish otoliths. *In* Otolith microstructure examination and analysis. *Edited by* D.K. Stevenson and S.E. Campana. Can. Spec. Publ. Fish. Aquat. Sci. **117**: 59–71.

Campana, S.E., and Jones, C.M. 1992. Analysis of otolith microstructure data. *In* Otolith microstructure examination and analysis. *Edited by* D.K. Stevenson and S.E. Campana. Can. Spec. Publ. Fish. Aquat. Sci. **117**: 73–100.

Campana, S.E., and Neilson, J.D. 1985. Microstructure of fish otoliths. Can. J. Fish. Aquat. Sci. **42**: 1014–1032.

Colton, J.B. Jr. 1978. Principal spawning areas and seasons of the Atlantic cod (*G. morhua*) in the Gulf of Maine and middle Atlantic Bight. Lab Rep. No. 78-66, National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, Mass.

Cushing, D.H. 1981. Fisheries biology, a study in population dynamics. 2nd ed. University of Wisconsin Press, Madison, Wis.

Cushing, D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. **26**: 249–293.

Dale, T. 1984. Embryogenesis and growth of otoliths in the cod (*Gadus morhua* L.). *In* The propagation of cod *Gadus morhua* L. Proceedings of an International Symposium, Arendal, Norway 1983. *Edited by* E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Institute of Marine Research, Flødevigan Biological Station, Arendal, Norway. pp. 231–250.

Davidson, F.J.M., and deYoung, B. 1995. Modelling advection of cod eggs and larvae on the Newfoundland Shelf. Fish. Oceanogr. **4**: 33–51.

Dunn, J.R. and Matarese, A.C. 1984. Gadidae: Development and relationships. *In* Ontogeny and systematics of fishes. *Edited by* H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall Jr., and S.L. Richardson. Special Publ. No. 1. American Society of Ichthyologists and Herpetologists. pp. 283–299.

Frank, K.T., Drinkwater, K.F., and Page, F.H. 1994. Possible causes of recent trends and fluctuations in Scotian Shelf/Gulf of Maine cod stocks. ICES Mar. Sci. Symp. **198**: 110–120.

Harden Jones. J.R. 1968. Fish migration. Arnold, London.

Helbig, J., Mertz, G., and Pepin, P. 1992. Environmental influences on the recruitment of Newfoundland/Labrador cod. Fish. Oceanogr. **1**: 39–56.

Hunter, J.R. 1981. Feeding ecology and predation of marine fish larvae. *In* Marine fish larvae, morphology, ecology and relation to fisheries. *Edited by* R. Lasker. University of Washington Press, Seattle, Wash. pp. 33–79.

Hutchings, J.A., Myers, R.A., and Lilly, G. 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 1–32.

Laurence, G.C., and Rogers, C.A. 1976. Effects of temperature and salinity on comparative embryo development and mortality of Atlantic cod (*Gadus morhua* L.) and haddock (*Melanogrammus aeglefinus* L.). J. Cons. Int. Explor. Mer, **36**: 220–228.

Lear, W.H., and Green, J.M. 1984. Migration of the "Northern" Atlantic cod and the mechanisms involved. *In* Mechanisms of migration in fishes. *Edited by* J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York. pp. 309–315.

Lear, W.H., and Wells, R. 1984. Vertebral averages of juvenile cod, *Gadus morhua*, from coastal waters of eastern Newfoundland and Labrador as indicators of stock origin. J. Northwest Atl. Fish. Sci. **5**: 23–31.

Methven, D.A., and Bajdik, C. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 78–90.

Myers, R.A., Mertz, G., and Bishop, C.A. 1993. Cod spawning in relation to physical and biological cycles of the northern Northwest Atlantic. Fish. Oceanogr. **2**(3/4): 154–165.

Pepin, P. 1989. Predation and starvation of larval fish: a numerical experiment of size- and growth-dependent survival. Biol. Oceanogr. **6**: 23–44.

Pepin, P. 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Can. J. Fish. Aquat. Sci. **48**: 503–518.

Pepin, P., Orr, D.C. and Anderson, J.T. 1997. Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Peterson, I., and Wroblewski, J.S. 1984. Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. **41**: 1117–1120.

Petrie, B., Loder, J.W., Lazier, J., and Akenhead, S.A. 1992. Temperature and salinity variability on the eastern Newfoundland shelf: the residual field. Atmos. Ocean. **30**: 120–139.

Pinsent, D.L. 1994. Hatch date and 0-group growth rate comparisons for cod (*Gadus morhua*) in Newfoundland waters: support for the match hypothesis. M.Sc. thesis, Memorial University of Newfoundland, St. John's, Nfld.

Radtke, R.L., and Waiwood, K.G. 1980. Otolith formation and body shrinkage due to fixation in larval cod (*Gadus morhua*). Can. Tech. Rep. Fish. Aquat. Sci. No. 929.

Schneider, D.C., Dalley, E., and Methven, D.A. 1997. Geographical contraction in a juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Scott, D.C.B. 1979. Environmental timing and the control of reproduction in teleost fish. Symp. Zool. Soc. Lond. **44**: 105–132.

Serebryakov, V.P. 1968. Cod reproduction in the northwest Atlantic. Fish. Res. Board Can. Transl. Ser. No. 1133.

Smedbol, R.K., and Wroblewski, J.S. 1997. Evidence for inshore spawning of northern Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, 1991–1993. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Stevenson, D.K., and Campana, S.E. (*Editors*). 1992. Otolith microstructure examination and analysis. Can. Spec. Publ. Fish. Aquat. Sci. No. 117.

Suthers, I.M., Frank, K.T., and Campana, S.E. 1989. Spatial comparison of recent growth in post-larval Atlantic cod (*Gadus morhua*) off southwestern Nova Scotia: inferior growth in a presumed nursery area. Can. J. Fish. Aquat. Sci. **46**(Suppl. 1): 113–124.

Svardson, G. 1949. Natural selection and egg number in fish. Inst. Freshwater Res. Drottningholm Rep. **29**: 115–122.

© 1997 NRC Canada

Templeman, W. 1981. Vertebral numbers in Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas, 1947–71, and their use for delineating cod stocks. J. Northwest Atl. Fish. Sci. **2**: 21–45.

Thompson, H. 1943. A biological and economic study of cod (*Gadus callarias*, L.) in the Newfoundland area. Nfld. Dep. Nat. Resour. Res. Bull. No. 14.

Wenner, C.A. 1983. Biology of the longfin hake, *Phycis chesteri*, in the western north Atlantic. Biol. Oceanogr. **3**: 41–75.

Yin, M.C., and Blaxter, J.H.S. 1987. Temperature, salinity tolerance and bouyancy during early development and starvation of Clyde and North Sea herring, cod and flounder larvae. J. Exp. Mar. Biol. Ecol. **107**: 279–290.

© 1997 NRC Canada

Detection of a recruitment signal in juvenile Atlantic cod (*Gadus morhua*) in coastal nursery areas

D.W. Ings, D.C. Schneider, and D.A. Methven

Abstract: In 1959–1964, Alistair Fleming conducted surveys of the abundance of Atlantic cod (*Gadus morhua*) in coastal Newfoundland waters for length classes corresponding to age 0 (post settlement), age 1, and age 2. An analysis of the data showed no correlation between catches in coastal water and cohort size reconstructed from catch data for the 2J3KL stock complex. Reanalysis was prompted by the finding that a recruitment signal could be detected on a nominal scale. Reanalysis of the 1959–1964 data showed that patterns of recruitment to a sequence of cohorts, at age 0, can be projected on a rank scale to age 1. Patterns at age 1 can similarly be projected on a rank scale to age 2. The 1959–1964 data combined with similar data from 1992–1994 showed that a recruitment signal could be detected with regression at the scale of 1 yr. The recruitment signal was more evident from a small number of sites that were visited frequently than from the complete set of sites. At currently low stock levels, the most reliable source of information on potential recruitment to cod stocks is a survey of coastal abundance combined with an offshore survey to measure degree of dispersion away from the coast.

Résumé : De 1959 à 1964, Alistair Fleming a réalisé des études sur l'abondance de la morue franche (*Gadus morhua*) dans les eaux côtières de Terre-Neuve pour des classes de tailles correspondant à l'âge 0 (après installation sur le fond), l'âge 1 et l'âge 2. Une analyse des données n'avait montré aucune corrélation entre les prises dans les eaux côtières et la taille des cohortes, déduite à partir des données sur les prises pour le complexe des stocks de 2J3KL. Une nouvelle analyse a été décidée quand il s'est avéré qu'un signal de recrutement pouvait être détecté sur une échelle nominale. La nouvelle analyse des données de 1959–1964 montre que les patrons de recrutement dans une série de cohortes, à l'âge 0, peuvent être projetés sur une échelle de rangs jusqu'à l'âge 1. De même, on peut projeter les patrons de l'âge 1 jusqu'à l'âge 2. Les données pour 1959–1964, combinées à des données similaires pour les années 1992–1994, montrent qu'un signal de recrutement peut être détecté à l'aide d'une régression sur l'échelle d'un an. Ce signal était plus marqué quand l'examen portait sur un petit nombre de sites visités fréquemment plutôt que lorsqu'il couvrait l'ensemble complet des sites d'observation. Dans la situation présente, où les stocks sont réduits, la source d'information la plus fiable quant au recrutement potentiel dans les stocks de morue est l'étude de l'abondance dans la zone côtière, combinée à une étude au large des côtes permettant de mesurer le degré de dispersion à partir de la côte.
[Traduit par la Rédaction]

Introduction

Mortality rates in fish are related to body size — as fish age and grow in size, mortality declines substantially. As a consequence, estimates of recruitment to fishable size-classes should become increasingly reliable as fish increase in size and experience lower natural mortality. Surveys of juvenile fish should, in theory, be more reliable than surveys of pelagic eggs and larvae (e.g., Peterman et al. 1988). Juvenile surveys have been used as an index of future recruitment to fishable size-classes in a number of groundfish species in Europe, notably European plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the North Sea (Rauck and Ziljstra 1978) and Atlantic cod (*Gadus morhua*) along the Norwegian coast (Tveite 1971, 1984). Despite their sound theoretical basis and their utility for groundfish in European waters, juvenile surveys are not used for groundfish assessment in the western North Atlantic.

A juvenile survey was undertaken for coastal Newfoundland by Alistair Fleming from 1959 to 1964, based on the observation that small fish were commonly seen in coastal waters, and on the assumption that the Labrador Current carried eggs and larvae from offshore spawning sites into coastal nursery areas. These data were analyzed by Lear et al. (1980) who found no correlation between number of juveniles in the Fleming surveys and total recruitment to age 3, based on reconstruction of 1959–1964 cohorts from catch data.

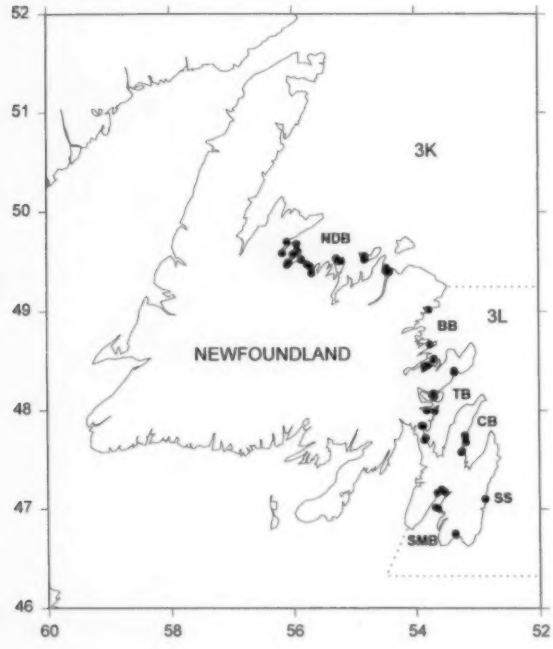
Several recent developments led us to undertake a reanalysis of these data. First, the assumption that eggs and larvae drift from offshore spawning grounds to coastal nursery areas has recently become tenable on physical grounds (deYoung and Davidson 1994). Hence, juvenile abundance in coastal water cannot be assumed to be decoupled from offshore production of larvae. Second, an analysis of the performance of a variety of gear types with juvenile fish in coastal waters (Methven and Schneider 1997) has shown that seines of the type used by Fleming can provide numbers that are valid on a

Received February 24, 1995. Accepted October 24, 1995.
J13232

D.W. Ings, D.C. Schneider, and D.A. Methven. Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada.

© 1997 NRC Canada

Fig. 1. Map of Newfoundland showing sites sampled by beach seines during 1959–1964 and NAFO divisions 3K and 3L. SMB = St. Mary's Bay, SS = Southern Shore, CB = Conception Bay, TB = Trinity Bay, BB = Bonavista Bay, and NDB = Notre Dame Bay.



relative scale, even though absolute numbers cannot be estimated. Third, an analysis of a subset of the Fleming data, standardized to only the first two sets at each beach, rather than all sets, showed that a recruitment signal was detectable (Schneider et al. 1997). Patterns of annual recruitment to coastal populations of cod within length group 0 were successfully predicted on a nominal scale (better or worse), given the ratio of two successive age classes in a prior year.

We undertook a reanalysis of the Fleming data to address several questions. (1) Can patterns of recruitment variability in a sequence of year-classes at one age be predicted from patterns in the previous year on a rank or ratio type of measurement scale? In other words, can a recruitment signal be detected on a rank or ratio type of scale, rather than just a nominal scale? (2) If this works at a time scale of 1 yr, do predictions of pattern across a sequence of year-classes hold up at time scales of 2 yr? (3) Can the pattern of recruitment across a sequence of length groups at age 3 (as measured for the entire stock) be predicted from the patterns observed in a sequence of length groups measured in beach seine surveys for the length class corresponding to age 2 fish?

Methods

Juvenile cod were collected in September and October of 1959–1964 (Lear et al. 1980). Approximately 45 sites were sampled each year from St. Mary's Bay in the south to Notre Dame Bay in the north (Fig. 1). Fish were collected with a 25-m beach seine (9-mm stretched mesh in the codend liner). Fish were assigned to three length groups: LG0 (standard length (SL) < 97 mm) corresponding to age 0, LG1 (SL = 97–192 mm) corresponding to age 1, and LG2 (SL > 193) corresponding to age 2. The survey was resumed in 1992, using the same sites and methods. Catches for the 1959–1964 and 1992–1994 surveys are reported as mean number per haul, based on two hauls at each site. Details are reported elsewhere (Schneider et al. 1997).

Estimates of cohort size at ages 3–6 for the 1959–1962 year-classes were obtained from a sequential population analysis (SPA) for the entire northeast Newfoundland cod stock (Baird et al. 1991) which assumed an instantaneous natural mortality rate of $M = 0.2$ and was calibrated to standardized research vessel surveys using the adaptive framework (Gavaris 1988). If it is assumed that the catch is known without error, then the estimates of abundance for the 1959–1962 cohorts are not sensitive to the calibration process and are therefore not impacted by the results of the research surveys.

Table 1 shows the beach seine catches (length groups 0, 1, and 2) together with population size estimates for ages 3, 4, 5, and 6 reconstructed from catch data, beginning with the 1959 cohort. To test whether projections could be made on a rank scale, the year-classes were ranked within each length group from large (1) to small (4) (Table 2). The change in ranking from one length group to another was computed by taking the sum of the absolute differences in ranks, as follows:

$$D_j = \sum_{i=1}^{4} |r_{ij} - r_{ij-1}|$$

where r_{ij} is the rank of year-class i at age j and r_{ij-1} is the rank of year-class i at the prior $(j - 1)$ age. The D_j statistic is zero if ranks of all year-classes remain the same from age $j - 1$ to the next age j. The observed values of D_j were small but not zero, so randomization tests (Manly 1991) were used to calculate the probability of obtaining the observed (small) differences in ranking by chance alone. Random permutations of the ranks in Table 2 were used to generate a set of D_j values. These D_j were then summed across age-classes to obtain an overall measure of change in ranking ΣD_j. The data were then randomized again to obtain another possible value of ΣD_j. This was repeated 400 times to obtain a frequency distribution of the statistic ΣD_j under the hypothesis of random change in ranking from year to year. This frequency distribution was used to calculate the probability of obtaining the observed value of ΣD_j by chance alone. Only the 1959–1964 cohorts were used in this analysis.

To test whether projections could be made on a ratio type of measurement scale, the catch of fish from a sequence of length groups at one age was regressed against the catch for the same length group in the previous year. A high explained variance in this analysis indicates little change in the size of one length group relative to another, and hence a strong recruitment signal from one year to the next. The assumptions for linear regression were checked by examining the residuals for normality. A criterion of $\alpha = 0.05$ was used to declare statistical significance in all analyses.

Results

There were small differences in rank between successive ages within year-classes (Table 2). The 1960 year-class, for example, had no difference in rank between length groups 1 and 2 and one difference in rank between length groups 2 and 3. However, at larger time intervals the difference in rank increased. For example, the 1960 year-class ranked second at length group 0, and then ranked fourth at age 3; the difference in rank was 2 from length group 0 to 3. Cursory examination of Table 2 suggested that ranks were relatively consistent at time scales of 1 yr, but less consistent at larger temporal scales.

© 1997 NRC Canada

Table 1. Mean annual beach seine catches (number per haul for length groups 0–2) and population size etimates (in millions for ages 3–6) for the 1959–1962 year-classes of northwest Atlantic cod.

	Seine catch for length-class			Population size for age-class			
Year	0	1	2	3	4	5	6
1959	178	5.17					
1960	31.4	134	0.588				
1961	11.0	27.7	2.07				
1962	29.5	6.96	0.813	725			
1963	17.8	30.7	0.439	641	586		
1964		50.8	2.06	880	519	455	
1965				1040	703	400	320
1966					847	549	285
1967						633	365
1968							428
1992	9.60	3.95					
1993	13.0	10.22	0.233				
1994	19.8	16.5	0.937				

Note: Only sites with two consecutive tows were used in calculating the mean seine catch. The number of beach sites used was 6 (1959), 17 (1960), 30 (1961), 40 (1962), 41 (1963), and 32 (1964). Beach seine catches from the east cost of Newfoundland are described by Lear et al. (1980). Population size estimates are from Baird et al. (1991).

Table 2. Ranked seine catches (length groups 0–2) and population size estimates (ages 3–6) for the 1959–1962 year-classes of northwest Atlantic cod.

	Ranked seine catch for length group:			Ranked population size for age-class:			
Year-class	0	1	2	3	4	5	6
1959	1	1	1	3	3	3	3
1960	2	3	3	4	4	4	4
1961	4	4	4	2	2	2	2
1962	3	2	2	1	1	1	1
Rank difference D_j	2	0	6	0	0	0	
Total rank difference $\Sigma D_j = 8$							

Note: Ranks (1 = largest, 4 = smallest) were derived for length groups from columns in Table 1. Rank difference D_j is the sum of the absolute differences in rank between adjacent (successive) length/age groups.

The degree of consistency was evaluated by computing ΣD_j, a measure of the consistency of ranking across several years. The year-to-year consistency across seven age-classes in Table 2 was fairly high: $\Sigma D_j = 2 + 0 + 6 + 0 + 0 + 0 = 8$. The chance of obtaining this degree of consistency by chance alone, based on randomization tests, was $p < 0.0025$. We concluded that the consistency of ranks was too great to be due to chance at the time scale of 1 yr for length groups 0–6.

A second randomization test was performed to determine the consistency of ranks from length groups 0–3. This was done because the interdependence of sequential estimates in SPA may have contributed to the consistency of ranks between ages 3–6. The year-to-year consistency was again high: $\Sigma D_j = 2 + 0 + 6 = 8$. The distribution of this statistic (this time summed from length groups 0–3 rather than from length groups 0–7) was again determined by randomization. The chance of obtaining this degree of consistency in rankings ($\Sigma D_j = 8$) by chance alone was $p = 0.0225$. We concluded that the consistency of rankings was significant at the time scale of 1 yr for length groups 0–3. A recruitment signal on a rank scale was detectible at time scales of 1 yr.

A further analysis was carried out to determine whether rankings remained consistent at time lags of 2 or 3 yr. The statistic D_j was calculated for length groups 0 versus 2, 1 versus 3 (2 yr lags), and 0 versus 3 (a 3 yr lag). The observed changes in ranking could have been obtained by chance. For length groups 0 versus 2, $D_j = 2$ ($p = 0.153$); for length groups 1 versus 3, $D_j = 6$ (p = 0.808). For length groups 0 versus 3, $D_j = 8$ (p = 0.808). We concluded that ranks did not remain consistent at time scales of 2 or 3 yr. A recruitment signal on

© 1997 NRC Canada

Table 3. Average count of three length groups per haul at sites sampled by A. Fleming (Lear et al. 1980) at least four times in six years (N_{hauls} = number of hauls; N_{sites} = number of sites).

		Count per haul			
Year	N_{hauls}	LG0	LG1	LG2	N_{sites}
1959	12	178	5.17	1.50	6
1960	24	41.1	135	0.0833	12
1961	36	8.78	36.5	2.78	18
1962	38	20.2	7.16	0.605	19
1963	38	20.0	50.9	0.237	19
1964	30	5.73	36.5	0.967	15

Table 4. Comparison of observed and predicted catches in 1993–1994, based on equations from the 1959–1964 data.

	Observed	Predicted
1993		
LG1	9.99	7.66
LG2	0.233	0.0798
1994		
LG1	16.5	10.4
LG2	0.937	0.202

a rank scale could not be detected at time scales of 2 or more yr.

Data from 1959–1964 and 1992–1994 were used to investigate whether a recruitment signal on a more detailed scale (ratio scale) could be detected. Regressions of LG1 abundances on LG0 abundances were significant (r^2 = 10746/11733 = 92%, $F_{1,5}$ = 54.43, $p < 0.001$). Analysis of residuals showed that this was affected by one pair of data points (1959 cohort). Removal of this observation raised the estimate of type I error (p = 0.298) and lowered the sensitivity of the test. A reanalysis was carried out using a nonnormal error structure (gamma distribution) according to the generalized linear model (McCullagh and Nelder 1989). The effect of this was to reduce the influence of the very high data point due to the 1959 cohort which resulted in a significant regression of LG1 on LG0 abundances (likelihood ratio test, Δdeviance = 4.59 due to adding regression parameter, df = 1, p = 0.032 computed from a χ^2 distribution). A recruitment signal on a ratio scale could not be detected when the 1959 cohort was removed, but could be detected when the influence of the 1959 cohort was adjusted by assuming a higher error for this cohort. When LG2 was regressed against LG1 the recruitment signal was almost significant (r^2 = 1.4507/2.6941 = 54%, $F_{1,5}$ = 5.83, p = 0.06). Examination of the residuals again indicated that a normal error structure could not be assumed. Reanalysis with a gamma error structure resulted in no significant recruitment signal (likelihood ratio test, Δdeviance = 1.884, df = 1, p = 0.28 calculated from χ^2 distribution). A more powerful test arises when the two analyses are combined (Δdeviance = 6.474, df = 2, p = 0.04). A recruitment signal from one year to the next, on a ratio scale, was detectable when two successive years were used. From length group 2 (beach seine) to age group 3 (cohort size reconstructed from catch data), there was no recruitment signal on a ratio scale (r^2 = 8.4%, $F_{1,2}$ = 0.18, p = 0.71).

As many sites as possible were used in this analysis to maximize sample size and hence increase sensitivity. Some sites were visited in a few years only, while others were visited in at least four of six years. In stratified random surveys of demersal fish, location changed from year to year, but this was not considered a problem for these mobile stages. However, catches of post-settlement juveniles showed a much higher degree of small-scale spatial consistency, a characteristic that made a recruitment signal harder to detect if survey locations were not the same each year. It was thus of interest to investigate whether the sensitivity of the analysis could be increased by restricting it to sites sampled in four of six years (Table 3), removing effects of spatial variability. Years 1992–1994 were omitted from the analysis so that a model based on the first five years could be tested against data not used in constructing the regression model. The regression of LG1 on LG0 catches was strongly significant ($F_{1,3}$ = 33.84, p = 0.01) with acceptable residuals. The regression of LG2 on LG1 catches was also strongly significant ($F_{1,3}$ = 450.3, p < 0.001), again with acceptable residuals. An iterative weighting algorithm was then used to estimate the parameters of the following equations:

$$LG1 = \beta_{0->1}\, LG0$$

$$LG2 = \beta_{0->1}\, LG1.$$

$\beta_{0->1}$ is the product of two quantities, the loss due to natural mortality $e^{-\mu t}$ during t = 1 yr and the ratio of catchabilities of LG1 and LG0 fish α_1/α_0. $\beta_{1->2}$ is the product of the loss due to natural mortality $e^{-\mu t}$ during t = 1 yr and ratio of catchabilities of LG2 and LG1 fish α_2/α_1. The estimates for the two composite parameters were

$\beta_{0->1}$ = 0.7984 SE = 0.1112

$\beta_{0->2}$ = 0.02019 SE = 0.00061.

The predictions from these equations for 1993 and 1994 were acceptable for LG1 (ratio of observed to predicted <2) but not for LG2 (ratio of observed to predicted >2) (Table 4). The underestimate of LG2 catches based on the 1959–1964 model is due either to a rise in the ratio of catchability α_2/α_1 or to a drop in mortality in recent years, compared with 30 yr ago.

Discussion

In their analysis of the 1959–1964 Fleming surveys, Lear et al. (1980) found no significant correlation between juvenile abundance and subsequent cohort size as reconstructed from catches over the entire area from Cape St. Mary's to central Labrador (2J3KL). Our reanalysis showed that within these data, there is a recruitment signal at time scales of 1 yr, on both ordinal (ranking) and interval scales of measurement. The recruitment signal was more readily detected with a small number of consistently positioned hauls than with a larger number of hauls that varied in location.

Given that a recruitment signal does carry through on a ratio scale from one year to the next in coastal populations of

© 1997 NRC Canada

juvenile cod, why did this not carry through to fishable stocks, at age 3? One possibility is that cohort strength reconstructed solely from catch data does not accurately represent true recruitment to the 2J3KL stocks. A related possibility is high type II error: four or five data points (as in Table 1 and in Lear et al. 1980) may simply have been too few to detect a relation that was present. Another possibility is that recruitment from nursery areas away from the coast swamped the coastal recruitment signal. There is not enough information on the abundance of juvenile cod away from the coast in the early 1960s to evaluate this.

The reported lack of a detectable recruitment signal from coastal juveniles to the entire stock in the 1960s, even if true, cannot be extrapolated to currently low stock conditions. The 1992 and 1993 year-classes at ages 0 and 1 were confined almost entirely to coastal waters (Dalley and Anderson 1995). Coastal nursery areas are at present the only substantial source of recruits to adult cod stocks. Because juveniles have been confined to coastal habitats, we predict that the recruitment signal currently evident in the coastal surveys will carry over to the entire stock, regardless of whether this signal carried through to the stock in the past.

Acknowledgements

This work was supported by funding under the Northern Cod Science Program from the Department of Fisheries and Oceans (DFO), St. John's. Catch data from beach seine surveys conducted by the late Alistair M. Fleming during 1959–1964 were provided by Edgar Dalley of the Science Branch (DFO). Tom Collier (DFO), a participant in the 1959–1964 surveys, contributed greatly by recalling many of the sites that were previously sampled as well as details of the sampling methods. We thank Claude Bishop, Stratis Gavaris (DFO), Manuel Gomes, and John Horne for discussion on sequential population analysis and Craig Tuck for producing Fig. 1. We thank E. Moksness and an anonymous reviewer for comments on a previous version of this manuscript.

References

Baird, J.W., Bishop, C.A., Brodie, W.B., and Murphy, E.F. 1991. An assessment of the cod stock in NAFO divisions 2J3KL. Can. Atl. Fish. Sci. Advis. Comm. Res. Doc. 91/53: 1–84.

Dalley, E.L., and Anderson, J.T. 1995. Distribution and abundance of demersal juvenile cod (*Gadus morhua*) in inshore and offshore areas of northeast Newfoundland (NAFO divisions 3KL) in the early 1990's. D.F.O. Atl. Fish. Res. Doc. 95/94.

deYoung, B., and Davidson, F. 1994. Modeling retention of cod eggs and larvae (*Gadus morhua* L.) on the Newfoundland shelf. ICES Mar. Sci. Symp. **198**: 346–355.

Gavaris, S. 1988. An adaptive framework for the estimation of population size. Can. Atl. Fish. Sci. Advis. Comm. Res. Doc. 88/29: 1–12.

Lear, W.H., Fleming, A.M., and Wells, R. 1980. Results of small cod surveys in eastern Newfoundland during 1959–64. Northwest Atl. Fish. Org. SCR Doc. 80/IX/144: 1–8.

Manly, B.F.J. 1991. Randomization and Monte Carlo methods in biology. Chapman and Hall, London.

McCullagh, P., and Nelder, J.A. 1989. Generalised linear models. 2nd ed. Chapman and Hall, London.

Methven, D.A., and Schneider, D.C. 1997. Gear independent patterns of variation in catch of juvenile cod (*Godus morhua*) in coastal habitats. Can. J. Fish. Aquat. Sci. **54**. (In press)

Peterman, R.M., Bradford, M.J., Lo, N.C.H., and Methot, R.D. 1988. Contribution of early life stages to interannual variability in recruitment of northern anchovy (*Engraulis mordax*). Can. J. Fish. Aquat. Sci. **45**: 8–16.

Rauck, G., and Ziljstra, J.J. 1978. On the nursery-aspects of the Waddensea for some commercial fish species and possible long-term changes. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **172**: 266–275.

Schneider, D.C., Dalley, E., and Methven, D.A. 1997. Geographic contraction in juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Tveite, S. 1971. Fluctuations in yearclass strength of cod and pollack in southeastern Norwegian coastal waters during 1920–1969. FiskeriDir. Skr. Ser. HavUnders. **16**: 65–76.

Tveite, S. 1984. 0-group cod investigations on the Norwegian Skagerrak coast. *In* The propagation of cod *Gadus morhua* L. *Edited by* E. Dahl, D.S. Danielssen, E. Mokness, and P. Solemdal. Flod. Rapp. **1**: 581–590.

© 1997 NRC Canada

Interaction between atmosphere, ice cover, and ocean off Labrador and Newfoundland from 1962 to 1992

S.J. Prinsenberg, I.K. Peterson, S. Narayanan, and J.U. Umoh

Abstract: The interannual variability of sea ice extent along the Labrador and Newfoundland coasts is shown to be caused by atmospheric circulation anomalies over the North Atlantic, typified by deviation in the strength of the Icelandic Low. During deepening of the Icelandic Low, stronger and more persistent northwesterly winds not only increase the southward ice flux but also cause abnormally low local air temperatures which increase local ice growth and decrease ice melt at the ice edge. The winter ice extent south of 55°N varies by as much as 65% about its 30-yr mean. Variations about the normal ice extent depend on air temperature and offshore wind anomalies in spring, but on alongshore wind anomalies in winter. The thickness of pack ice and landfast ice are determined by fall and winter air temperatures, and by snow conditions. A high ice extent, long ice season, and low spring air temperatures are all associated with cold oceanic water temperatures observed over the Labrador and Newfoundland shelves and low surface salinity water inshore at Station 27 during the subsequent summer. In contrast, low winter air temperatures are associated with high surface salinity water in the spring.

Résumé : Nous démontrons ici que la variabilité, d'une année à l'autre, de l'extension de la glace de mer le long des côtes du Labrador et de Terre-Neuve est causée par des anomalies dans la circulation atmosphérique au-dessus de l'Atlantique Nord, anomalies caractérisées par des écarts dans la profondeur de la dépression d'Islande. Lorsque la dépression d'Islande se creuse, des vents du nord-ouest plus forts et plus persistants entraînent non seulement une augmentation du flux de la glace vers le sud, mais également des températures locales de l'air anormalement basses, ce qui a pour effet d'augmenter la croissance de la glace dans la région et de réduire la fonte sur le front des glaces. L'extension de la glace en hiver au sud du 55°N varie dans des proportions pouvant aller jusqu'à 65% de la valeur moyenne établie sur 30 ans. Les écarts par rapport à l'extension normale résultent au printemps des anomalies dans la température de l'air et dans les vents de terre, mais en hiver dépendent des anomalies dans les vents parallèles à la côte. L'épaisseur de la banquise et de la glace de rive est déterminée par les températures de l'air à l'automne et en hiver, de même que par les conditions d'enneigement. Une grande extension, une saison des glaces prolongée et de basses températures de l'air au printemps, toutes ces circonstances sont associées à de basses températures de l'eau de mer sur les plateaux continentaux du Labrador et de Terre-Neuve l'été suivant, et à une faible salinité de l'eau de surface enregistrée le long de la côte à la Station 27, à la même période. Par opposition, de basses températures de l'air en hiver sont associées à une salinité élevée de l'eau de surface au printemps.
[Traduit par la Rédaction]

Introduction

Although global air temperatures were above normal for most of the 1980s and early 1990s (Jones 1994), the Labrador/Newfoundland area experienced below-normal temperatures for most of this period (Drinkwater et al. 1992). Severe ice conditions and abnormally cold water temperatures occurred along the Labrador and Newfoundland coasts during the cold years, suggesting an interdependence of atmospheric, ice cover, and oceanographic properties.

Coupling between atmospheric and ice cover properties in the Labrador Sea has been investigated for many years. Smith (1927) found high correlations between iceberg numbers and ice extent off Newfoundland with the winter barometric pressure gradient across the Labrador Sea. More recently, Walsh and Johnson (1979) and Chapman and Walsh (1993) described long-term anomalies of ice extent in various Arctic regions, with ice extent anomalies in the North Atlantic being out of phase with those over the rest of the Arctic. Similarly, Agnew (1993) found that during winters with weak Aleutian and Icelandic lows, heavy ice years occurred for the Arctic as a whole but light ice conditions occurred over the Davis Strait/Labrador Sea area.

Ocean water and ice cover properties are strongly interrelated. The cross-sectional area of the cold intermediate layer (CIL, water with temperatures <0°C) is larger following cold winters with extensive ice coverage (Petrie et al. 1988). The seasonal cycle of salinity on the Labrador and Newfoundland shelves depends on local ice melt (Petrie et al. 1992; Myers et al. 1990) and on the freshwater flux from Baffin Bay and Hudson Bay (Prinsenberg 1988). Mysak and Manak (1989) and Mysak et al. (1990) have suggested that high ice extent

Received December 30, 1994. Accepted October 26, 1995.
J13230

S.J. Prinsenberg and I.K. Peterson. Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.
S. Narayanan and J.U. Umoh. Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

© 1997 NRC Canada

anomalies in the Greenland Sea are advected into Baffin Bay and Labrador Sea, where they result in negative salinity anomalies. In turn, salinity anomalies in the Greenland and Labrador seas may have caused extreme ice conditions there during the late 1960s and early 1970s (Marsden et al. 1991).

These results show a strong relationship between atmospheric, ice cover, and ocean properties, suggesting that anomalies of one property should not be studied in isolation. This paper examines in detail the interaction of ice cover with the ocean and atmosphere for the Labrador/Newfoundland Shelf area. After describing the data sources, the interannual variability of ice extent and ice thickness and their dependence on atmospheric variability are examined, followed by a discussion of the effects of atmospheric and ice cover properties on oceanographic conditions.

Data sources

The pack ice data used in this study were derived by digitizing weekly composite ice charts (1963–1992) produced by the Ice Centre (Environment Canada); the period from 1963 to 1988 is described in Peterson and Prinsenberg (1990). The dataset consists of concentrations of five ice categories (new, grey, grey–white, first-year, and old) on a 0.5° latitude by 1.0° longitude grid. These data are used to compute (1) ice extent, the total surface area within the ice edge, (2) ice area, the total area of the ice itself, and (3) ice volume. First-year ice includes all ice (except multiyear) thicker than 30 cm, and its mean thickness is assumed to be 100 cm; thus, estimates of ice volume are subject to large errors. However, the relative proportions of thin versus thick ice categories indicate the relative importance of local ice growth versus ice advection. Weekly landfast ice and snow thickness data for Cartwright Harbour were also obtained from the Ice Centre (Environment Canada), while the iceberg data were obtained from the International Ice Patrol (Groton, Conn.).

Geostrophic winds for the Labrador and Newfoundland shelves were provided by the Atmospheric Environment Service and were computed from gridded 6-h pressure data obtained from the Fleet Numerical Oceanographic Centre (Swail 1985). Monthly and mean winter alongshore and offshore wind components were then calculated assuming an offshore direction of 35° for two offshore grid points, designated as Stations 9 and 13 (Fig. 1) by Drinkwater and Pettipas (1993). The North Atlantic Oscillation Index (NAO), defined as the difference in mean sea level air pressure between the Azores and Iceland, describes much of the variability of winter winds (Rogers 1984); the NAO index data were provided by K. Drinkwater (personal communication). Mean daily air temperature data for the coastal stations Cartwright, Bonavista, and St. John's (Fig. 1) were obtained from the Atmospheric Environment Service. The daily mean temperatures were used both directly and to calculate freezing degree-days.

Two oceanographic datasets were used to examine the interannual variability of water properties over the Newfoundland Shelf and were obtained from the Department of Fisheries and Oceans, St. John's, Nfld. The first consisted of summer temperature profiles collected since the late 1940s from a transect off Bonavista Bay; from this the more densely sampled period of 1962–1992 was used. The second dataset (1946–1992) consisted of temperature and salinity data collected about twice a month at standard depths at Station 27, a 175-m-deep monitoring station 8 km offshore of St. John's. Detailed description and analyses of both oceanographic datasets can be found in Petrie et al. (1992), Narayanan et al. (1992, 1995), Drinkwater et al. (1992), Colbourne and Senciall (1993), and Colbourne and Fitzpatrick (1994). Since winter temperature and salinity observations on the Labrador Shelf are scarce, under-ice CTD data collected in March 1994 over Hamilton Bank are also presented; the data were collected through augered ice holes using a Seabird SBE-25 CTD probe.

Interannual ice cover variability

The interannual variability of the amount of ice covering the northeastern Newfoundland Shelf between 49°N and 51°N (Fig. 2) was calculated from the weekly values for February, March, and April when ice extent is at a seasonal maximum. Ice extent (time series *a*) is the surface of the ocean within the ice edge, while ice area (time series *b*) excludes the open-water areas within the ice edge. Except for southern regions, the differences between ice extent and ice area were small because most of the ice was of high concentration. Although ice area is mostly composed of thin, locally grown ice, ice volume (time series *c*) is mostly composed of thick ice (>30 cm). Ice extent and ice area were similar in 1972 and 1973, but ice thickness and volume were lower in 1972 than in 1973. Less ice extent, area, and volume were present during the warm winters of the late 1960s than during the cold winters of the early 1970s, mid-1980s, and early 1990s.

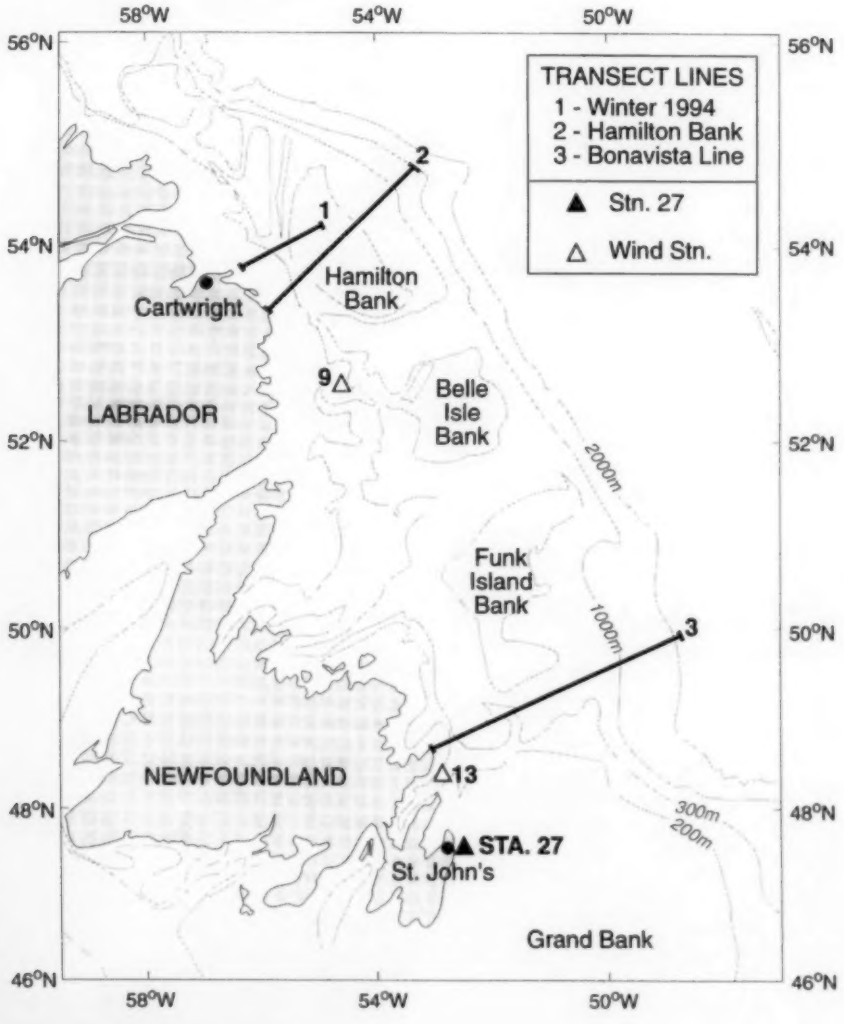
The mean monthly ice extent, as well as the minimum and maximum observed for each month over the 30-yr period for three 2° latitude bands (Fig. 3), clearly showed that monthly variability was higher in southern areas. When the 30-yr monthly means were subtracted from the observed values, monthly ice extent anomalies were produced (Fig. 4) which showed positive peaks in the early 1970s, mid-1980s, and early 1990s, about 12 and 6 yr apart. In an analysis of a 101-yr record of winter sea level pressure for the eastern North Atlantic, Kelly (1977) observed sea level energy peaks centred at periods of 11, 5.0, 3.4, and 2.2 yr, although only those at 11 and 2.2 yr were significant. Variations in the timing of the arrival and retreat of the ice cover were evident (Fig. 4).

The mean winter ice extent south of 55°N (Fig. 5) varied as much as 65% (1.5×10^5 km^2) about the 30-yr mean of 2.25×10^5 km^2. If one assumes that the average thickness of the pack ice is 1 m, then the heat required to melt the pack ice is equivalent to that needed to warm a 30 m oceanic surface layer by 2.5°C. With a 65% variation in ice cover extent, this would translate into a variability in the ocean surface layer temperature of 1.5°C due to the variability in ice cover.

Correlations between ice extent and several environmental variables are shown for winter (December–March, Table 1) and spring (April–June, Table 2). Although the tables were based on 29 yr of data, there were only about 13 independent data points for winter ice extent based on autocorrelations, so that r values less than 0.55 were not significant. As suggested by the time series plots (Fig. 2), ice extent, ice area, and ice volume were highly correlated (r = 0.86–0.96). Correlations with other variables are discussed in the following sections.

© 1997 NRC Canada

Fig. 1. Map of the Newfoundland and Labrador coasts showing the bathymetry, place names, and locations of the Hamilton Bank (1 and 2) and Bonavista (3) transects and geostrophic wind stations.



Strong northwesterly winds increased ice extent off Labrador and Newfoundland both by advecting more ice southwards and by advecting cold Arctic air which enhanced ice growth. The potential effect of ice drift was shown as follows. Assuming a drift rate of 1.8% of the geostrophic wind speed and no turning angle (Peterson and Symonds 1988), the monthly net alongshore and offshore ice drifts were calculated by assuming an offshore direction of 35° (Fig. 6). The net alongshore winter ice drift (January–March) due to wind varied 200 km·mo^{-1} about a mean of 250 km·mo^{-1} at Station 9 on the southern Labrador shelf (Fig. 7). Over the three winter months, this caused a variability in ice flux of 1.2×10^5 km^2 for the 200-km-wide mid-Labrador Shelf. Thus the variability in ice drift due to wind alone could account for 80% of the variability in ice extent seen below 55°N.

When severe ice conditions occurred in the early 1970s and early 1990s, strong local northwesterly winds were evident, while weak winds occurred during the mild late 1960s (Figs. 6 and 7). However, there was no evidence of strong alongshore winds in the mid-1980s, corresponding to the third period of severe ice conditions. The NAO index, in contrast, did show a peak in the mid-1980s (Fig. 5) when northwesterly winds were strong to the north over the Baffin Bay and Labrador Sea area (Drinkwater and Pettipas 1993). In spite of this, the correlation of winter ice extent with local northwesterly winds ($r = 0.74$, Table 1) was still somewhat higher than with the large-scale wind field represented by the NAO index ($r = 0.64$). Offshore (northeasterly) winds in winter along the Labrador and Newfoundland shelves were positively correlated with pack ice parameters, although for the Labrador Shelf the correlation was not significant. Thus, offshore

© 1997 NRC Canada

Fig. 2. Interannual variability of winter means (Feb.–Apr.) of (*a*) ice extent and ice area, (*b*) total and thin ice (<30 cm) areas, and (*c*) total and thin ice volumes for the northeastern Newfoundland Shelf area between 49°N and 51°N (based on digitized Ice Centre (Atmospheric Environment Service) weekly composite ice charts).

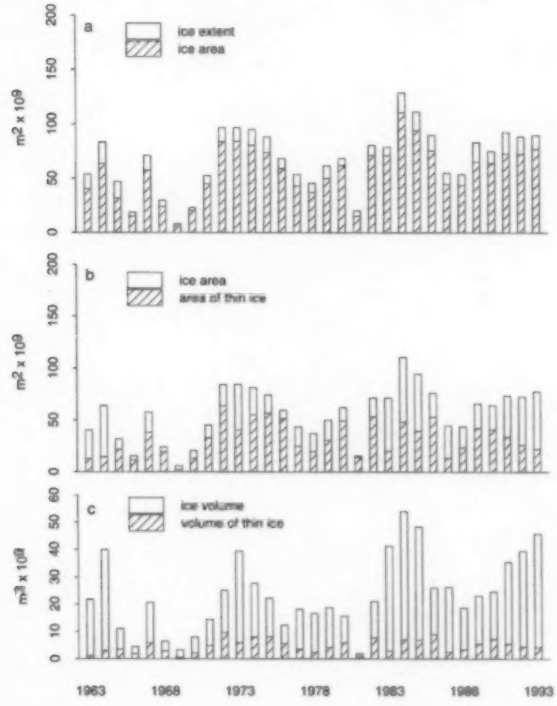
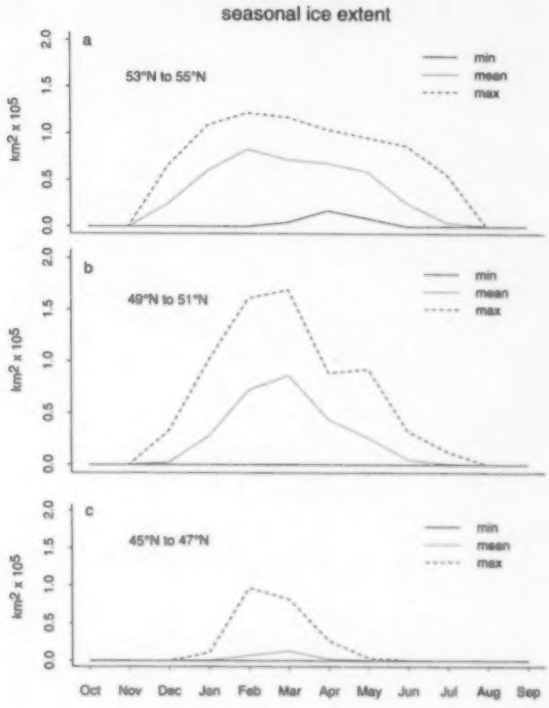


Fig. 3. Thirty-year monthly mean, maximum, and minimum ice extent for three 2° latitude bands across the Labrador/Newfoundland Shelf (based on weekly composite ice charts).



winds appeared to increase ice severity over the Newfoundland Shelf during the ice edge advance, not decrease it through increased offshore ice melt. Offshore winds may open leads where new ice can form, and reduce internal ice pressure which enables ice to move southwards faster in the area influenced by the Labrador Current.

Correlations of winter ice extent were higher with air temperature than with winds (Table 1), as found by Walsh and Johnson (1979) in a larger scale study. Correlations of winter ice extent were higher with air temperature at Cartwright than at St. John's (Fig. 8), and with northwesterly winds off Labrador than off Newfoundland, presumably because of southward ice advection.

Unlike in winter, spring ice extent and air temperatures were not significantly correlated with northwesterly winds or with the NAO (Table 2). There was a significant correlation between spring air temperature at Cartwright and ice extent ($r = -0.67$). However, Walsh and Johnson (1979) showed that it is not clear during ice melt whether air temperature or ice extent occurs first whereas during ice growth, air temperature leads ice extent. The correlation between spring ice extent and winter ice extent ($r = 0.66$) indicated the high degree of persistence, again consistent with Walsh and Johnson (1979). Marko et al. (1994) showed that the spring ice extent is also highly correlated with the winter ice extent in Davis Strait.

Interannual ice thickness variability

Landfast ice in Cartwright Harbour (mid-Labrador Shelf, Fig. 1) usually begins to form near the beginning of December and reaches a mean ice thickness of 84 cm in March (Atmospheric Environment Service 1992). It continues to grow to 92 cm in April, partly as a result of the melting and refreezing of snow, and decays in May or June. The persistence of monthly mean ice thickness anomalies was high from December to April, with correlation coefficients of 0.78–0.89 for 1-mo lags. Mean March ice thicknesses were low in the late 1960s and high in 1973 and the mid-1980's, with an overall standard deviation of 17 cm (Fig. 9*a*).

The expected mean ice thickness based on air temperatures was estimated using a freezing degree-day model (Anderson 1961). Assuming a freeze-up date of December 1 and mean Cartwright air temperatures for December, January, and February (−9.6, −13.7, and −13.2°C), the predicted ice thickness on March 1 was 76 cm compared with an observed thickness of 77 cm.

Correlations of March ice thickness with monthly mean air temperatures at Cartwright were higher for the early winter period of September–January ($r = -0.34$ to -0.53) than for the monthly winter temperatures of February ($r = -0.21$) or March ($r = -0.14$). The early mean air winter temperature of September–January explained 53% of the variance of March ice thickness. Cold temperatures in the fall would produce an

© 1997 NRC Canada

Fig. 4. Time series of the monthly ice extent anomalies (deviations from the 30-yr means) for the same three 2° latitude bands as in Fig. 3.

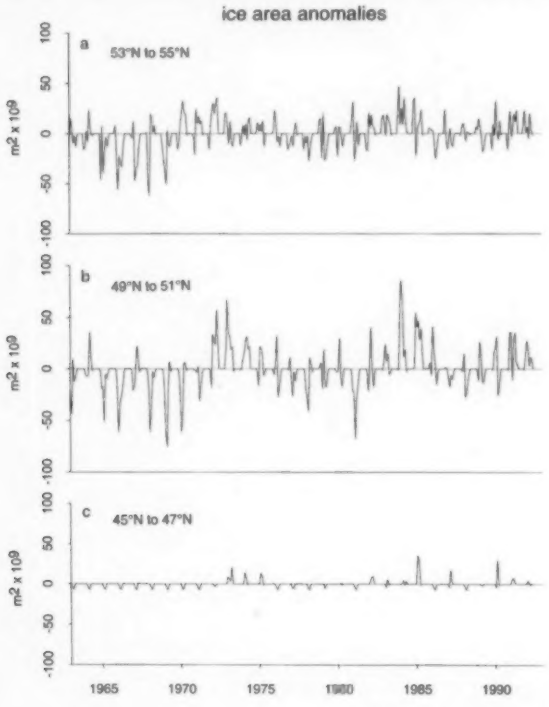
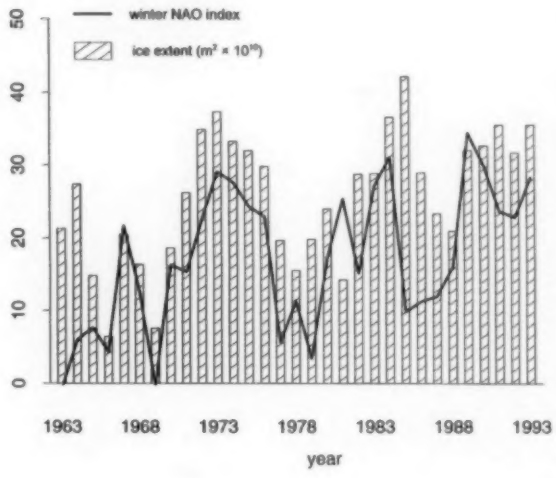


Fig. 5. Time series of the mean winter ice extent (Feb.–Apr.) south of 55°N and winter mean North Atlantic Oscillation (NAO) index (K. Drinkwater, personal communication).



earlier freeze-up, while cold temperatures in December and January would increase ice growth.

The low degree of correlation with February and March air temperatures may be due to the thick snow layer found in those months (23 ± 14 cm in February and 29 ± 15 cm in March). A thick snow layer insulates the ice cover and reduces the effect of air temperature on ice growth (Prinsenberg 1992). Since snow depths are small in the early winter (Atmospheric Environment Service 1992), this is not the case, and the snow cover will not impede ice growth and air temperature anomalies can produce ice thickness anomalies (Prinsenberg 1992). However, late winter snow depths along the Labrador coast are extremely large and in fact can depress the ice below the water surface. This was observed at Hopedale (just north of Cartwright): brine and seawater infiltrated the bottom of the snow layer to form a slush layer (Weeks and Lee 1958). This layer subsequently refroze, thereby adding 12 cm to the ice cover after a single storm. A similar refrozen slush layer was observed at Cartwright in March 1991 when the ice surface was found to be 22 cm above the original ice surface layer observed 2 mo earlier in January (Prinsenberg and Peterson 1992).

If a frozen slush layer has formed on the ice surface, then the new ice surface is at the ice–water interface and the ice is in hydrostatic equilibrium with the snow layer. Thus, as shown by Ackley et al. (1990), the thickness of the snow layer $h_s = (\rho_w - \rho_i)h_i/\rho_s$ where h_i is the thickness of the ice and ρ_w, ρ_i, and ρ_s are the densities of seawater, ice, and snow, respectively. Taking $\rho_w = 1.0 \times 10^{-3}$ g·cm^{-3}, $\rho_i = 0.9 \times 10^{-3}$ g·cm^{-3}, and $\rho_s = 0.3 \times 10^{-3}$ g·cm^{-3} (Mellor 1977) with h_i = 0.76 m on March 1, then the predicted value of h_s is 0.25 m, compared with an observed h_s of 0.26 m, i.e., the climatological mean values for ice and snow thickness suggest that surface ice accretion occurs due to snow loading.

Southern Labrador has the highest maximum depth of snow and the highest annual snowfall in eastern Canada (Fisheries and Environment Canada 1978). From December to February, Cartwright has a total rain-equivalent precipitation of 0.24 m (88% of which is snow). This is equivalent to 0.80 m of snow, 0.26 m of which was found on the ice on March 1, leaving 0.56 m which had either sublimated or was flooded to form ice.

Sublimation in the winter period (December–February) was estimated as $E = 0.622\rho C_e u(r_h e_{sa} - e_{so})/p_o$ where ρ = 1.2 kg·m^{-3} is the air density, $C_e = 1.75 \times 10^{-3}$ is the transfer coefficient for latent heat, u = 6.2 m·s^{-1} is the wind speed, r_h = 0.81 is the relative humidity, e_{sa} = 3.50 mbar (1 mbar = 100 Pa) is the saturation vapour pressure of air at 10 m, and e_{so} = 2.25 mbar is the saturation vapour pressure at the snow surface. Based on ice temperature measurements in 1991 (Prinsenberg and Peterson 1992), the snow surface temperature was assumed to be 5°C higher than the mean air temperature (−11.6°C). Thus, sublimation, E, was estimated as 12 cm·mo^{-1}, or 36 cm between December and February, leaving 20 cm which had been flooded to form ice. This suggests that 26% of the ice on March 1 had been formed from surface flooding.

The partial correlation coefficient of March ice thickness with total precipitation (September–January) after removing the effect of air temperature (September–January) was 0.63 (the correlation between precipitation and air temperature was only −0.11). Thus, in a regression model of March ice thickness, the fraction of the variance explained increased from 53% with air temperature to 71% when total precipitation (December–February) was included (Fig. 9*a*). The

© 1997 NRC Canada

Table 1. Correlation coefficient (r) between winter atmospheric, ice cover, and summer oceanographic parameters (icebergs are the yearly total).

		Ice drift				Ocean CIL		Pack ice		
		9		13						
Winter	NAO	SE	NE	SE	NE	Area	Temp.	Volume	Area	Extent
Icebergs	+0.54	+0.53	+0.13	+0.39	+0.38	+0.72	+0.63	+0.74	+0.68	+0.66
NAO Index	1.00	+0.73	+0.12	+0.49	+0.40	+0.53	−0.63	+0.50	+0.66	+0.64
AirT Cartwright		−0.81	−0.24	−0.61	−0.38	−0.41	+0.32	−0.74	−0.85	−0.84
AirT St. John's		−0.78	+0.16	−0.75	−0.17	−0.24	+0.02	−0.52	−0.69	−0.70
SE ice drift 9		1.00	+0.16	+0.83	+0.48	+0.29	−0.19	+0.60	+0.77	+0.74
NE ice drift 9			1.00	−0.05	+0.64	+0.01	−0.17	+0.10	+0.22	+0.30
SE ice drift 13				1.00	+0.48	+0.23	+0.01	+0.55	+0.66	+0.66
NE ice drift 13					1.00	+0.22	−0.35	+0.48	+0.56	+0.59
CIL area						1.00	−0.76	+0.64	+0.56	+0.58
CIL temp.							1.00	−0.53	−0.54	−0.53
Ice volume								1.00	+0.84	+0.86
Ice area									1.00	+0.96
Ice extent										1.00

Note: NOA, North Atlantic Oscillation, CIL, cold intermediate layer, airT, observed air temperatures. Since autocorrelation analysis indicates 13 effective independent points, only r values greater than 0.55 are significant at the 95% level.

Table 2. Correlation coefficient (r) between spring atmospheric, spring and winter ice cover, and summer oceanographic parameters.

		Ice drift				Ocean water					
		9		13		27		CIL		Pack ice extent	
Spring	NAO	SE	NE	SE	NE	Temp.	Salinity	Area	Temp.	Spring	Winter
Winter NAO	+0.14	+0.10	−0.10	−0.05	−0.07	−0.34	+0.03	+0.53	−0.14	+0.40	+0.64
Spring NAO	1.00	+0.65	+0.45	+0.48	+0.45	+0.14	−0.11	−0.01	+0.06	−0.08	+0.25
AirT Cartwright		−0.10	+0.39	−0.25	−0.20	+0.26	+0.18	−0.35	+0.15	−0.67	−0.37
AirT St. John's		−0.23	+0.50	−0.40	+0.19	+0.40	−0.13	−0.01	−0.18	−0.29	−0.17
NE ice drift 9		1.00	+0.16	+0.73	+0.16	−0.20	+0.26	−0.07	+0.19	+0.07	+0.22
SE ice drift 9			1.00	−0.12	+0.53	+0.31	−0.25	+0.07	−0.02	−0.42	−0.05
NE ice drift 13				1.00	+0.18	−0.00	+0.35	−0.19	+0.34	+0.04	+0.06
SE ice drift 13					1.00	+0.48	−0.38	−0.15	+0.11	−0.14	+0.09
Station 27 temp.						1.00	−0.28	−0.59	+0.34	−0.63	−0.52
Station 27 salinity							1.00	−0.27	+0.41	−0.05	−0.05
CIL area								1.00	−0.76	+0.62	+0.52
CIL temp.									1.00	−0.67	−0.53
Winter ice volume										+0.70	+0.88
Winter ice extent										+0.66	1.00

Note: NOA, North Atlantic Oscillation, CIL, cold intermediate layer; airT, observed air temperature. Since autocorrelation analysis indicates 13 effective number of independent points, only r values greater than 0.55 are significant at the 95% level.

regression coefficient for total precipitation implied that there was 0.87 m of additional ice produced for each metre of additional precipitation. Although freezing degree-day models can incorporate the effect of the insulation of the snow layer (Prinsenberg 1992), they cannot as yet account for ice formation due to slush layers.

Although data for studying interannual variability of ice thickness were available from landfast stations such as Cartwright, ice thickness data from the pack ice were sparse. A rough measure of the mean thickness of offshore ice, however, was obtained by dividing the ice volume (February–April) by the ice area (Fig. 9*b*). Pack ice thicknesses were high in 1963–1964, the mid-1980s, and the early 1990s and low in the early 1980s. While there were some similarities with the Cartwright landfast ice thickness (Fig. 9*a*), the agreement was not high. The proportion of thick ice should increase the earlier the freeze-up, although other factors were clearly involved such as offshore advection, ice divergence, and rafting.

© 1997 NRC Canada

Fig. 6. Monthly time series of alongshore and offshore ice drift components derived from predicted (Atmospheric Environment Service) geostrophic winds over the Labrador Shelf at Station 9.

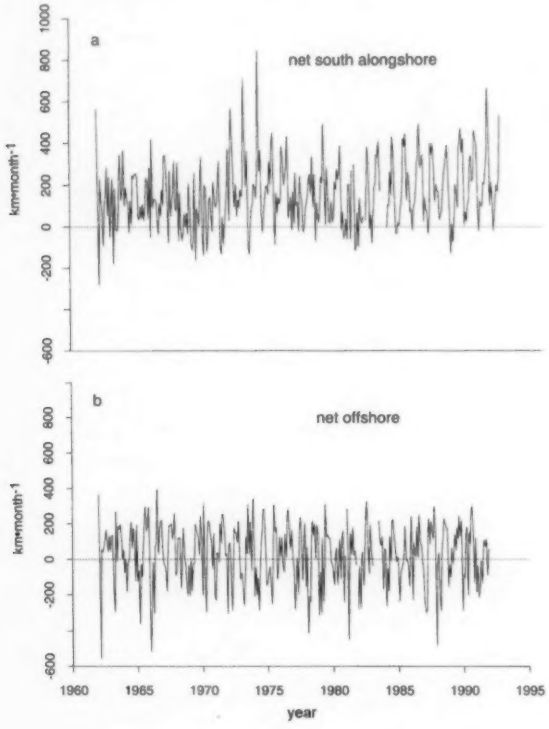
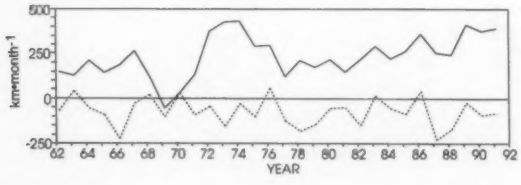


Fig. 7. Winter alongshore (net south, solid line) and offshore (net offshore, broken line) ice drift components derived from predicted (Atmospheric Environment Service) geostrophic winds for Labrador Shelf Station 9.



The variation in the start of spring ice melt was estimated from the anomaly of spring temperature (March and early April) over the 30-yr period. Since the average air temperature increases at 1.1°C·wk^{-1} in the spring, an anomaly of 1.8°C represented a time delay or advance of about 1.5 wk for the advent of spring ice melt. During May, the atmospheric heat input to the ocean at this latitude is 150 W·m^{-2} or 300 cal·cm^{-2}·d^{-1}(Smith and Dobson 1984). A 10-d delay in ice retreat represented a heat loss to the ocean equivalent to a 1°C decrease in water temperature over 30 m.

Shelf water properties

Water properties over the Labrador Shelf (Fig. 10*b*) showed

Fig. 8. Freezing degree-days (FDD) time series for Cartwright, Bonavista, and St. John's based on observed (Atmospheric Environment Service) air temperatures.

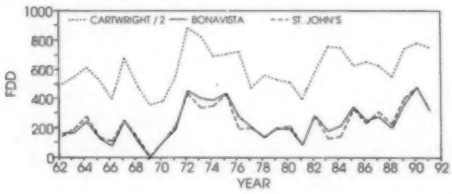
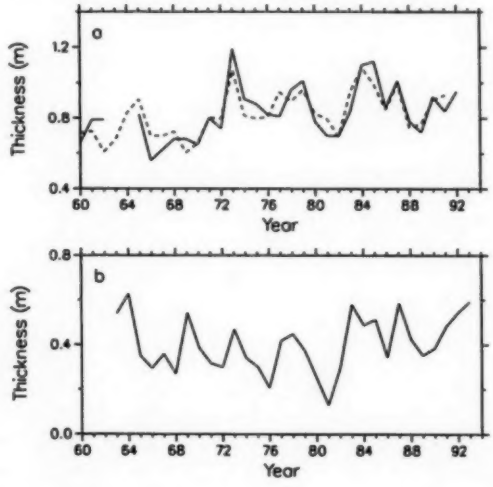


Fig. 9. (*a*) March ice thicknesses in Cartwright Harbour as observed (solid line) by the Ice Centre (Atmospheric Environment Service) and as predicted (broken line) from Sept.–Jan. air temperatures and Dec.–Feb. total precipitation. (*b*) Mean Feb.–Apr. ice thickness of offshore ice from 49°N to 51°N based on digitized Ice Centre (Atmospheric Environment Service) weekly composite ice charts.



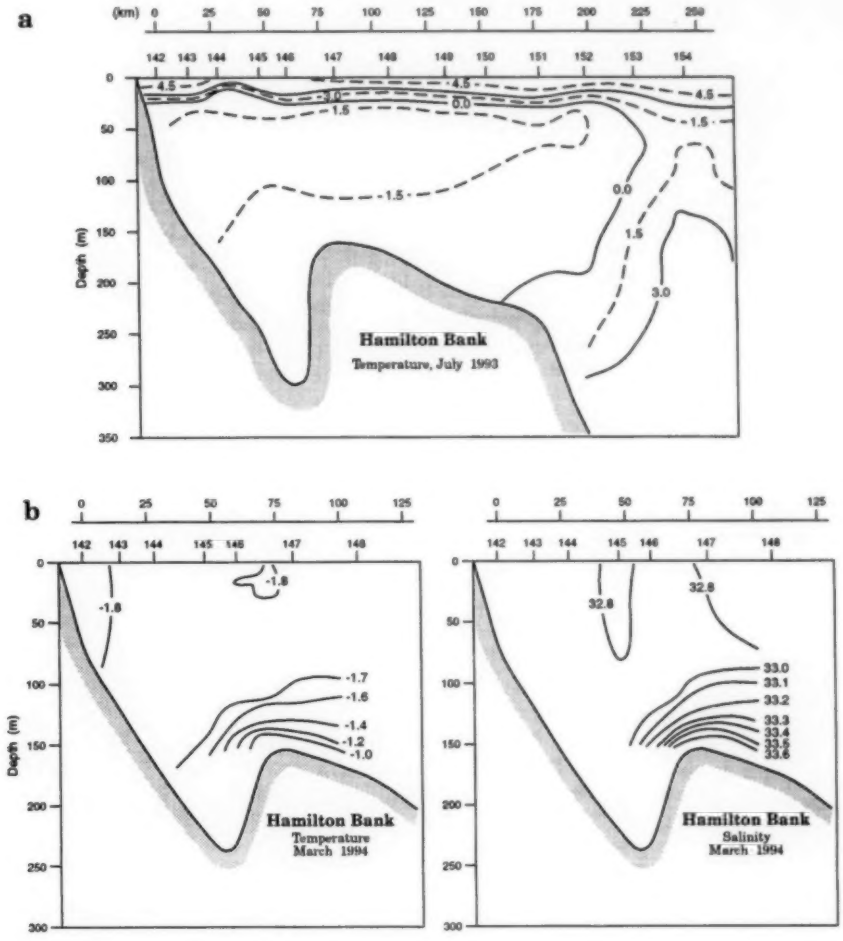
that in winter, inshore under-ice temperatures were near the freezing point throughout the entire water column, while offshore over Hamilton Bank, slightly warmer saltier water was found at depth. Summer temperatures (Fig. 10*a*) from the same area in July 1993 showed the large extent of the CIL below the shallow warmer surface layer.

When the cross-sectional areas of the CIL were larger than normal, the mean temperatures for the 50–100 m water column (the core of the CIL) were also lower (Fig. 11). Large CIL areas occurred in the three cold periods, as shown by Petrie et al. (1992), Colbourne and Senciall (1993), and Narayanan et al. (1995). Overall, the CIL area anomaly varied as much as 75% about its mean of 28×10^6 m^2 during these periods; this variation represents an 80-m layer for the 350-km transect line or one third of the total water column. The summer CIL area, CIL temperature, and the spring surface layer (0–50 m) water temperature at Station 27 were significantly correlated with spring ice extent (Table 2), in agreement with Petrie et al. (1988).

The low correlations between air temperature and spring surface temperature and salinity in Table 2 may have arisen

© 1997 NRC Canada

Fig. 10. Hamilton Bank cross-sections of (*a*) summer temperature field (July 1993) and (*b*) winter salinity and temperature fields (March 1994).



because the water properties were averaged over depth and time, and lags were not taken into account. Spring surface temperature and salinity anomalies at Station 27 for a single time (April 1) and depth (20 m) (Fig. 12) were linearly interpolated to April 1, close to the time of the year when minimum surface temperature, maximum surface salinity, and southernmost ice extent occurred. They were measured at 25 m before 1959 and at 20 m after 1959. The time series were negatively correlated ($r = -0.51$), with periods of low salinity/warm temperature during 1951–1954 and 1968–1971. Anomalous years were 1983, 1984, and 1991 when low salinity/cold temperature water was observed.

Correlations of April surface water temperature and salinity were obtained with air temperatures at Cartwright and St. John's where the air temperatures were averaged over periods of 1–4 mo ending on March 31 (Table 3). All correlations were significant at the 95% level, based on effective number of independent observations calculated using the formula in Garrett and Toulany (1981). For water temperature, the correlation was highest with Cartwright December–March mean air temperature (0.79), while for salinity, the correlation was highest with St. John's February–March air temperature ($r = -0.79$). The autocorrelations at lags of 1, 2, and 3 yr were –0.07, 0.23, and 0.00 for salinity and −0.10, 0.16, and −0.04 for St. John's February–March air temperature. These were consistent with the 2.2-yr cycle Kelly (1977) observed in air pressure data for the eastern North Atlantic which may be a manifestation of the quasi-biennial oscillation.

The fact that sea surface temperature appeared to respond to air temperature over a time scale of about 4 mo was in agreement with the fact that surface water temperatures were better correlated with air temperatures upstream at Cartwright. A 3-mo transit time between Cartwright and St. John's is equivalent to a current speed of about 0.1 $m \cdot s^{-1}$. However, the response of salinity appeared to be local and the correlation with air temperature was not improved by using an averaging period longer than 2 mo. The time series for air temperature anomalies (Fig. 12) showed that in the low-salinity and low-temperature years of 1983, 1984, and 1991, the St. John's February–March air temperature anomaly was pos-

© 1997 NRC Canada

Table 3. Correlation coefficients (r) between April 1 surface temperature and salinity (parameter 1) and air temperatures (AirT) (parameter 2) for different periods of the year at St. John's and Cartwright.

Parameter 1	Parameter 2	Dec.–Mar.	Jan.–Mar.	Feb.–Mar.	Mar.
Station 27 temp.	AirT St. John's	0.68	0.69	0.62	0.57
Station 27 temp.	AirT Cartwright	0.79	0.72	0.63	0.50
Station 27 salinity	AirT St. John's	–0.78	–0.77	–0.79	–0.69
Station 27 salinity	AirT Cartwright	–0.53	–0.52	–0.57	–0.49

Fig. 11. Extent of the summer (July–Aug.) cold intermediate layer (CIL) and 50–100 m layer temperature along the Bonavista transect (line 3 in Fig. 1).

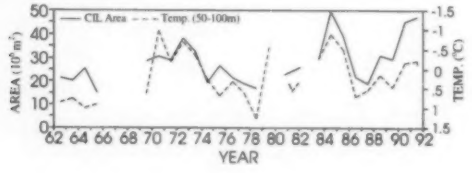
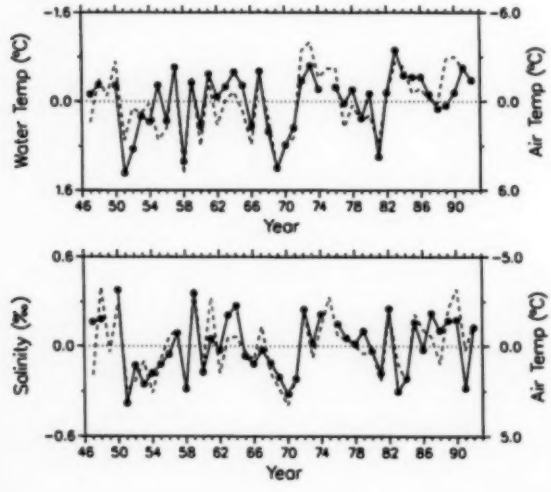


Fig. 12. April near-surface (20 m) temperature and salinity anomalies (deviations from the 1946–1992 means of 32.39‰ and −0.97°C) at Station 27. Broken lines are Cartwright Dec.–Mar. air temperatures (upper panel) and St. John's Feb.–Mar. air temperatures (lower panel), those being the periods which produced the highest correlations (Table 3).



itive, while the Cartwright December–March temperature anomaly was negative.

A strong negative relationship between summer surface salinity at Station 27 and ice extent on the Labrador Shelf was reported by Myers et al. (1990). They also suggested that spring (March–April) surface salinity anomalies are determined by summer runoff from Hudson Bay in the previous summer, and that low salinities observed around 1971 may have been due to the "Great Salinity Anomaly". However, the correlations in Table 3 suggest that spring surface salinity anomalies at Station 27 may be determined instead by local air temperature.

The high correlation between air temperature and surface salinity may simply be due to increased sea ice melt from warm air temperatures. Station 27 lies close to the position of the median ice edge, so that in some years the ice would melt to the north and in other years to the south. A total interannual range of surface salinity of 0.8 ppt (Fig. 12) corresponds to 1 m of sea ice with a salinity of 8‰ mixing in 32 m of surface water with a salinity of 33‰, which is reasonable.

Other factors may contribute to the high correlation between air temperature and surface salinity. Low air temperatures would reduce the negative heat flux from water, thus increasing convective mixing. This would ultimately result in ice growth and increased convective mixing associated with brine rejection from the growing ice. High air temperatures would also increase runoff from snow and ice melt on land. Low temperatures are associated with higher wind speeds, which would also cause increased mixing, and higher evaporation. High temperatures are associated with onshore winds, which would trap ice inshore where it would melt.

Conclusions

Although the existence of sea ice along the Canadian coast results from favourable oceanographic conditions, the interannual variability in sea ice conditions was shown to be caused by the variability in the large-scale atmospheric circulation which locally manifested itself as air temperature and wind anomalies. Severe midwinter ice conditions occurred during years with deep Icelandic Lows when stronger and more persistent northwesterly winds increased the southwards ice transport along the Canadian coast and when colder air temperatures increased local ice growth and decreased local ice melt. Spring ice extent correlated more with ice dispersion processes than ice advection as seen by the correlation with air temperature and offshore wind frequency. The winter ice extent south of 55°N varied by as much as 65% about its 30-yr mean of 2.25×10^5 km^2, significantly affecting marine transportation and salmon, capelin, and northern cod fisheries.

In general, the correlations were consistent with the findings of a larger scale study by Walsh and Johnson (1979), in that correlations of ice extent are higher with air temperature than with air pressure patterns (NAO), and the persistence of ice extent is higher than that of wind. In addition, as found also by Marko et al. (1994), ice extent was more highly correlated with air temperature and winds to the north than to the

© 1997 NRC Canada

south, presumably because of southward advection. The pack ice parameters showed a general decrease in correlation values from ice extent to ice area and finally to ice volume. This decrease is probably due to error in the estimation of concentration and ice type, not to the physical processes involved.

The interannual variability of the landfast ice thickness at Cartwright was more strongly correlated with fall than with winter temperatures as the thick snow layer by midwinter isolated the ice cover from atmospheric effects. Snowfall appeared to increase ice thickness by causing flooding of the ice surface with brine and seawater and subsequent freezing of this slush layer.

A strong correlation existed between the local air temperature and Station 27 surface salinity in the early spring over 46 yr due to anomalies in the local ice melt. Thus, there appears to be no need to invoke the advection of the "Great Salinity Anomaly" to explain the decrease in surface salinity in 1968–1971, although it may be important elsewhere or at greater depths.

Acknowledgements

The authors would like to thank K. Drinkwater and J. Loder for their comments on the first draft of the manuscript and T. Wright and T. van der Baren for assisting in the analysis. The research is funded through the Federal Panel of Energy, Research and Development.

References

Ackley, S.F., Lange, M.A., and Wadhams, P. 1990. Snow cover effects on Antarctic sea ice thickness. *In* Sea ice properties and processes. Proceedings of the W.F. Weeks Sea Ice Symposium. *Edited by* S.F. Ackley and W.F. Weeks. CRREL Monogr. 90-1: 16–21. Cold Regions Research and Engineering Laboratory, U.S. Corps of Engineers, Hanover, N.H.

Agnew, T. 1993. Simultaneous winter sea-ice and atmospheric circulation anomaly patterns. Atmos.-Ocean, **31**(2): 259–280.

Anderson, D.L. 1961. Growth of sea ice. J. Glaciol. **3**: 1170–1172.

Atmospheric Environment Service. 1992. Ice thickness climatology, 1961–1990 normals. Rep. Ice 2–91. Ice Centre, Atmospheric Environment Services, Environment Canada, Ottawa, Ont.

Chapman, W.L., and Walsh, J.E. 1993. Recent variability of sea ice and air temperature in high latitudes. Bull. Am. Meteorol. Soc. **74**: 33–47.

Colbourne, E., and Fitzpatrick, C. 1994. Temperature, salinity and density at Station 27 from 1978 to 1993. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 159.

Colbourne, E., and Senciall, D. 1993. Temperature, salinity and density along the standard Bonavista transect. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 150.

Drinkwater, K.F., and Pettipas, E.G. 1993. Climate data for the Northwest Atlantic: surface wind stresses off eastern Canada, 1946–1991. Can. Data Rep. Hydrogr. Ocean Sci. No. 123.

Drinkwater, K.F., Petrie, B., and Narayanan, S. 1992. Overview of environmental conditions in the Northwest Atlantic in 1991. NAFO SCR Doc. 92/73.

Fisheries and Environment Canada. 1978. Hydrological atlas of Canada. Fisheries and Environment Canada, Ottawa, Ont.

Garrett, C., and Toulany, B. 1981. Variability of the flow through the Strait of Belle Isle. J. Mar. Res. **39**: 163–189.

Jones, P.D. 1994. Hemispheric surface air temperature variations: a reanalysis and an update to 1993. J. Clim. **7**: 1794–1802.

Kelly, P.M. 1977. Solar influence on North Atlantic mean sea level pressure. Nature (Lond.), **269**: 320–322.

Marko, J.R., Fissel, D.B., Wadhams, P., Kelly, P.M., and Brown, R.D. 1994. Iceberg severity off eastern North America: its relationship to sea ice variability and climate change. J. Clim. **7**: 1335–1351.

Marsden, R.F., Mysak, L.A., and Myers, R.A. 1991. Evidence for salinity enhancement of sea ice in the Greenland and Labrador seas. J. Geophys. Res. **96**: 4783–4789.

Mellor, M. 1977. Engineering properties of snow. J. Glaciol. **19**(81): 15–66.

Myers, R.A., Akenhead, S.A., and Drinkwater, K. 1990. The influence of ice melt and Hudson Bay runoff on the salinity of the inner Newfoundland shelf. Atmos.-Ocean, **27**: 241–256.

Mysak, L.A., and Manak, D.K. 1989. Arctic sea-ice extent and anomalies, 1953–1984. Atmos.-Ocean, **27**: 376–405.

Mysak, L.A., Manak, D.K., and Marsden, R.F. 1990. Sea-ice anomalies observed in the Greenland and Labrador Seas during 1901–1984 and their relation to an interdecadal Arctic climate cycle. Clim. Dyn. **5**: 111–133.

Narayanan, S., Prinsenberg, S., and Colbourne, E.B. 1992. Overview of environmental conditions in 2J3KL NAFO subareas in 1991. NAFO SCR Doc. 92/6.

Narayanan, S., Carscadden, J., Dempson, J.B., O'Connell, M.F., Prinsenberg, S.J., Reddin, D.G., and Shackell, N. 1995. Marine climate off Newfoundland and its influence on Atlantic salmon (*Salmo salar*) and capelin (*Mallotus villosus*). *In* Climate change and northern fish populations. *Edited by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. No. 121: 461–474.

Peterson, I.K., and Prinsenberg, S.J. 1990. Sea ice fluctuations in the western Labrador Sea (1963–1988). Can. Tech. Rep. Hydrogr. Ocean Sci. No. 123.

Peterson, I.K., and Symonds, G. 1988. Ice floe trajectories off Labrador and eastern Newfoundland: 1985–1987. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 104.

Petrie, B., Akenhead, S., Lazier, J., and Loder, J. 1988. The cold intermediate layer on the Labrador and Northeast Newfoundland shelves, 1978–86. NAFO Sci. Counc. Stud. **12**: 57–69.

Petrie, B., Loder, J.W., Akenhead, S., and Lazier, J. 1992. Temperature and salinity variability on the eastern Newfoundland shelf; the residual field. Atmos.-Ocean, **30**: 120–139.

Prinsenberg, S.J. 1988. Ice ridge contributions to the freshwater contents of Hudson Bay and Foxe Basin. Arctic, **41**: 6–11.

Prinsenberg, S.J. 1992. Effect of the snow cover on the ice growth rates at land-fast ice stations in the Canadian Arctic. IAHR92. Proc. 11th Int. Symp. Ice, **2**: 633–644.

Prinsenberg, S.J., and Peterson, I.K. 1992. Newfoundland Shelf Sea Ice Program, 1991. Can. Tech. Rep. Hydrogr. Ocean. Sci. No. 141.

Rogers, J.C. 1984. The association between the North Atlantic Oscillation and the Southern Oscillation in the Northern Hemisphere. Mon. Weather Rev. **112**: 1999–2015.

Smith, E.H. 1927. International ice observation and ice patrol service in the North Atlantic Ocean. Season of 1926. U.S. Coast Guard Bull. No. 15.

Smith, S.D., and Dobson, F.W. 1984. The heat budget at Ocean Weather Station *Bravo*. Atmos.-Ocean, **22**: 1–22.

Swail, V.R. 1985. Geostrophic wind climatology of Canadian marine areas. Can. Clim. Cent. Rep. 85–9.

Walsh, J.E., and Johnson, C.M. 1979. An analysis of Arctic sea ice fluctuations, 1953–77. J. Phys. Oceanogr. **9**: 580–591.

Weeks, W.F., and Lee, O.S. 1958. Observations on the physical properties of sea-ice at Hopedale, Labrador. Arctic, **11**: 135–156.

© 1997 NRC Canada

Hydrography and baroclinic circulation in the Scotian Shelf region: winter versus summer

John W. Loder, Guoqi Han, Charles G. Hannah, David A. Greenberg, and Peter C. Smith

Abstract: Salient features of the climatological seasonal hydrography and baroclinic circulation over the Scotian Shelf and adjacent shelf regions are described using a historical temperature–salinity database and a diagnostic circulation model. Emphasis is placed on the contrast between winter and summer, surface and bottom temperature and salinity, and the depth-integrated baroclinic (and associated barotropic) transports. The computed fields indicate that the overall regime is dominated by the equatorward flow of relatively cool and fresh shelf water from the Gulf of St. Lawrence and Newfoundland Shelf. However, submarine banks, basins, and cross-shelf channels have pronounced "topographic-scale" influences on both the hydrography and circulation, such as distinct contrasts in bottom temperature between banks and basins, Slope Water inflows in channels, and anticyclonic (cyclonic) circulation tendencies over banks (basins). The major channels in combination with major coastline indentations result in a gradual progression of regional hydrographic regimes, from the Newfoundland Shelf to the Middle Atlantic Bight. The general robustness and realism of the large- and topographic-scale hydrographic and circulation features on the Scotian Shelf and in the Gulf of Maine suggest that the historical database is adequate for a useful quantitative description in these areas.

Résumé : Les principales caractéristiques de l'hydrographie climatologique saisonnière et de la circulation barocline au-dessus de la plate-forme néo-écossaise et des plateaux adjacents sont décrites à l'aide d'une base de données chronologiques sur la température et la salinité, et d'un modèle diagnostique de la circulation. Nous soulignons les contrastes qui existent entre l'hiver et l'été, de même que les différences dans la température et la salinité de surface et de fond, et dans les transports baroclines (et transports barotropes associés) intégrés sur la verticale. Les zones évaluées indiquent que le régime global est dominé par un courant constitué d'eau relativement froide et douce, provenant du golfe du Saint-Laurent et de la plate-forme de Terre-Neuve, et se dirigeant vers l'équateur. Cependant, la présence de bancs et de bassins sous-marins, et de chenaux qui traversent les plates-formes, a des effets marqués à l'échelle topographique à la fois sur l'hydrographie et sur la circulation — effets tels que de nets contrastes dans la température de fond entre les bancs et les bassins, des venues d'eau de pente dans les chenaux, et des tendances à une circulation anticyclonique au-dessus des bancs et cyclonique au-dessus des bassins. La présence des principaux chenaux, combinée à celle des découpures importantes de la côte, crée une progression graduelle de régimes hydrographiques régionaux, de la plate-forme de Terre-Neuve jusqu'au golfe médio-atlantique. Le caractère généralement solide et concret des caractéristiques de la circulation et de l'hydrographie, à l'échelle globale et à l'échelle topographique, sur la plate-forme néo-écossaise et dans le golfe du Maine, laisse à penser que l'utilisation de bases de données chronologiques est adéquate pour une description quantitative utile dans ces régions.
[Traduit par la Rédaction]

Introduction

The Scotian Shelf and adjacent regions (Fig. 1) have large spatial and temporal variations in hydrographic properties, primarily associated with their location (*i*) in the confluence zone of the North Atlantic subpolar and subtropical gyres (e.g., Loder et al. 1996), (*ii*) downstream of the St. Lawrence River system (e.g., Sutcliffe et al. 1976), and (*iii*) in a mid-latitude continental lee where air–sea fluxes have strong annual cycles and vertical mixing has marked variability (e.g., Umoh and Thompson 1994). On the physical oceanographic side, these variations are intimately connected to circulation and mixing, while on the biological side, the hydrographic structure can have both direct and indirect influences on fish populations. Many studies have contributed to the present-day description and understanding of the hydrographic regime and its physical and biological implications, but only limited attention has been directed towards the three-dimensional (3-D) spatial structure of the region-wide climatological hydrography and the associated baroclinic circulation.

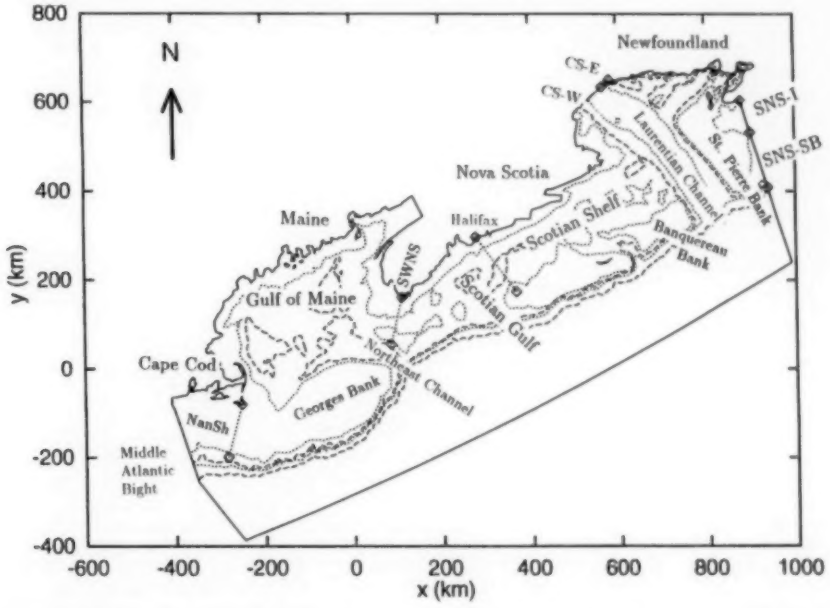
In recent years, larger and more readily available historical hydrographic datasets and numerical circulation models have provided new opportunities for improving the quantitative description of 3-D hydrography and circulation on the continental shelf. In this paper, we use a historical temperature and salinity database assembled at the Bedford Institute of Oceanography (K.F. Drinkwater and co-workers, personal communication, 1994) and a 3-D diagnostic circulation model (Lynch et al. 1992; Naimie and Lynch 1993) to examine two

Received February 2, 1995. Accepted January 11, 1996.
J13305

J.W. Loder, D.A. Greenberg, and P.C. Smith. Department of Fisheries and Oceans, Bedford Institute of Oceanography, P.O. Box 1006, Dartmouth, NS B2Y 4A2, Canada.
G. Han. Department of Oceanography, Dalhousie University, Halifax, NS B3H 4J1, Canada.
C.G. Hannah. Oceadyne Environmental Consultants, Bedford, NS B4A 3M2, Canada.

© 1997 NRC Canada

Fig. 1. Map showing the model domain together with bathymetry, feature locations, and transport section locations in the study region extending from the southern Newfoundland Shelf to the Middle Atlantic Bight. The origin is at 42°N, 67°W. The isobaths shown are 100, 200, 400, and 1000 m. The diamonds indicate endpoints of sections for which transports are given in Tables 1 and 2: inner (SNS-I) and shelf-break (SNS-SB) segments of the southern Newfoundland Shelf, western (CS-W) and eastern (CS-E) segments of Cabot Strait, and Halifax (Halfx), southwestern Nova Scotia (SWNS), and Nantucket Shoals (NanSh).



aspects of the climatological physical oceanographic regime in the greater Scotian Shelf region (Fig. 1): (1) the horizontal structure of the surface and bottom temperature and salinity distributions, and their seasonal changes, and (2) the seasonal baroclinic circulation with emphasis on the poorly studied eastern Scotian Shelf region where strong influences are expected from both the Gulf of St. Lawrence (via Cabot Strait) and the southern Newfoundland Shelf (across Laurentian Channel). The goal of the hydrographic component is to illustrate the broad- and topographic-scale horizontal structure, in order to help establish the climatological setting of particular areas of biological importance (e.g., fish spawning and nursery areas on submarine banks). The goals of the circulation component are more exploratory: to examine the potential of diagnostic circulation models in the data-sparse eastern Scotian Shelf region, to identify the possible pathways for inflows from upstream, and to examine the associated sensitivities of the circulation in downstream regions. In both components, we contrast winter and summer seasons to show the seasonal changes. For temperature, these seasons reflect the broad-scale minima and maxima of the well-known annual surface variation (e.g., Mountain and Manning 1994; Umoh and Thompson 1994); for salinity, they approximate the periods of minimum and maximum freshwater outflow through Cabot Strait (Sutcliffe et al. 1976). The hydrographic and eastern Scotian Shelf emphases complement those in Hannah et al. (1996), which focuses on the seasonal variation of baroclinic circulation on the Scotian Shelf proper and in the Gulf of Maine, and in Naimie et al. (1994) and Lynch et al. (1996) which examine composite seasonal circulation in the Georges Bank and Gulf of Maine regions, respectively.

We start with a brief summary of the database, the procedure for estimating hydrographic fields, and the circulation model. The hydrographic results are then presented, followed by those for the circulation modelling. The latter comprise, first, the identification of barotropic pathways and then the evaluation of baroclinic flow fields. We conclude with a brief discussion.

Methods

The analysis and modelling approach and procedures are similar to those used in Hannah et al. (1996), to which the reader is directed for further detail.

Temperature and salinity database

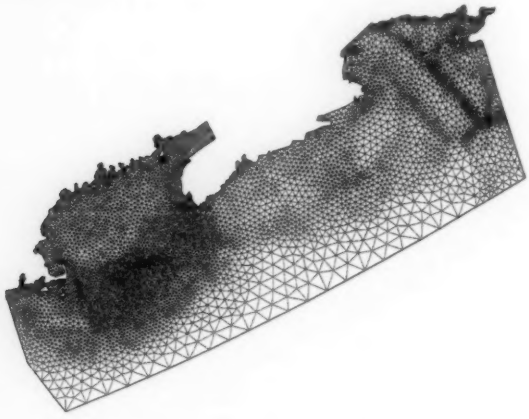
The historical hydrographic database comprises about 54 000 stations with coincident temperature and salinity observations (CTD profiles, and bottle-sample salinities with reversing-thermometer temperatures), mostly scattered between 1950 and 1990. Station positions are distributed across the Scotian Shelf and adjacent regions, ranging from 38 to 48°N and from 53 to 72°W, with poorest coverage generally in winter and in eastern and offshore areas. After standard quality control and subsampling of the CTD data (10-m intervals for 0–60 m, 25-m intervals for 75–250 m, 50-m intervals for 300–500 m, and 100-m intervals below), density profiles were computed, yielding a database of temperature, salinity, and density observations for positions in four-dimensional (4-D) space (two horizontal coordinates, depth and time).

Grid and optimal interpolation

Mean temperature, salinity, and density fields for climatological winter and summer seasons were estimated from the database using 4-D optimal linear interpolation (Bretherton et al. 1976). This procedure provides estimates of the mean fields at specified grid points in

© 1997 NRC Canada

Fig. 2. ss2 horizontal finite-element grid used for the hydrographic fields and in the numerical model (see Fig. 1 for feature locations and distance scale).



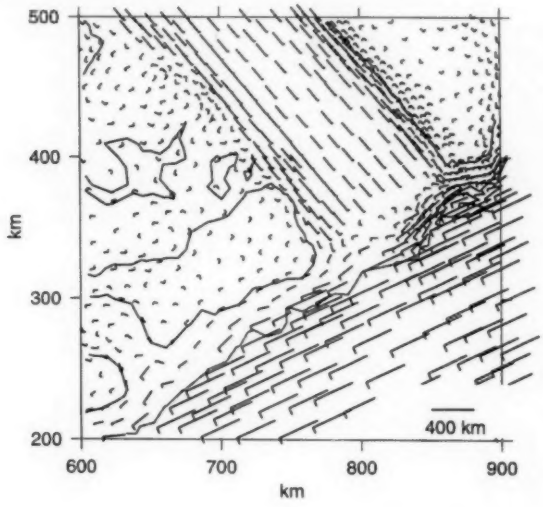
4-D space, from their nearest-neighbour data points based on separation distances scaled by specified correlation scales in an assumed covariance function (see Appendix). Only the 50 nearest neighbours were used in the optimal interpolation, so the key feature of the correlation scales summarized below is the relative magnitudes for the four independent coordinates.

The horizontal grid points were the nodes of a triangular finite-element mesh extending along-shelf from the Burin Peninsula (Newfoundland) to Long Island (New York) (Fig. 2). The mesh (ss2) has open boundaries across Cabot Strait and the upper Bay of Fundy (as well as across the shelf and offshore) and extends 100–200 km beyond the shelf break to the region of Gulf Stream influences (Fig. 1). It is a hybrid of two grid-generation strategies. For the Scotian Shelf and Gulf of Maine (and adjoining offshore areas), the grid is the gb3 mesh used in Greenberg et al. (1996) and Hannah et al. (1996) with highest resolution in shallow areas, particularly those in the Gulf of Maine. To allow examination of the Laurentian Channel region, a southern Newfoundland Shelf mesh (sns2) is attached with highest resolution in areas of smallest topographic length scale ($h/|\nabla h|$) where the strongest mean currents generally occur. The merged mesh has 8949 nodes, with realistic water depths (h) shoreward of the 1000-m isobath, and a false bottom in the deep ocean which slopes gently to 1200 m at the offshore boundary. The vertical grid points for the estimated fields were levels of constant depth, corresponding to the subsampling depths of the CTD data. The fields were also estimated at levels below the seafloor, with vertical interpolation then used to obtain values at the seafloor.

Time grid points (essentially season midtimes) were chosen in consideration of the known annual hydrographic variations, the circulation results of Hannah et al. (1996) (where bimonthly periods were examined), and density data coverage on the southern Newfoundland Shelf (where data sparsity is particularly severe). February 1 and August 1 were selected for the winter and summer midtimes, respectively, with data from all years then used in estimating the climatological fields. Temporal correlation scales of 45 and 30 d were used for winter and summer, respectively, considering the poorer data coverage in winter.

An important issue in the estimation of the hydrographic fields is the choice of appropriate spatial correlation scales, particularly in view of known spatial inhomogeneities (e.g., imposed by the pronounced bathymetry), the generally sparse dataset, and temporal variability at various frequencies. Horizontal anisotropy in the horizontal correlation scales was parametrically specified from the local values of h and ∇h, using a recently available implementation of

Fig. 3. Along- and cross-isobath (shelf/channel) horizontal correlation scales used in the base-case density field estimation for the outer Laurentian Channel region (coordinates are the same as in Fig. 1). The base of each orthogonal line pair is at a node on the ss2 grid (Fig. 2), and the line lengths are proportional to the local correlation scales. The 100- and 1000-m isobaths are also shown.



optimal interpolation (I. He, G. Boudreau, and R. Hendry, Bedford Institute of Oceanography, personal communication, 1994). The base-case specification (Appendix and Fig. 3) is similar to that in the sensitivity cases (gb3) presented by Hannah et al. (1996). Isotropic scales of 40 and 30 km were used for uniform-depth shelf areas in winter and summer, respectively, and increased (decreased) scales were specified in the along- (cross-) isobath directions taken from ∇h. The along-isobath scales increase to 100–200 km over the upper continental slope and then increase further to approximate the deep-ocean along-shelf (65°T) scale of 400 km. In contrast, the cross-isobath scales decrease to 15–20 km over the upper slope and then increase again to approximate the deep-ocean cross-shelf scale of 60 km. The one difference of the present base case from Hannah et al. (1996) is the specification of additional anisotropy in the Laurentian Channel ($h > 200$ m): along- and cross-channel scales of 150 and 15 km, respectively, to reflect the channel geometry in areas of weak bottom slope. Finally, the vertical correlation scales were specified to increase with depth below the surface, ranging from 15 m in the upper 60 m to 200 m at 1200 m depth. Examination of the sensitivity of the estimated hydrographic fields to the details of the specification of the correlation scales indicates a generally weak sensitivity for the broad- and topographic-scale shelf features, but stronger influences on local baroclinic circulation features (also see Hannah et al. (1996). However, the deep-ocean hydrographic and circulation fields are only crude representations, with the large anisotropic horizontal scales intended to smooth the sparsely sampled Slope Water region in the along-shelf direction.

Circulation modelling

The resulting 3-D hydrographic fields provide valuable insight into the seasonal-mean circulation, both in "tracing" the full circulation in the vicinity of hydrographic (e.g., freshwater) sources and allowing estimation of the internal pressure gradients that drive the baroclinic flow component.

An initial indication of the baroclinic circulation tendency in the associated pressure field is provided by the two dimensional (2-D) steric height field which gives the relative surface elevation at all

© 1997 NRC Canada

locations under the assumption that the bottom geostrophic velocity is small everywhere. We estimated the steric height field using Sheng and Thompson's (1996) approximation method with a reference depth of 1200 m (also see Hannah et al. (1996). This method gives a unique but approximate estimate of steric height by using a domain-averaged relation between bottom density and water depth. The associated baroclinic circulation tendency is surface flow along steric height isolines with high steric values to the right.

The barotropic advective pathways in the Laurentian Channel region and the total 3-d circulation associated with the baroclinic pressure fields were examined using FUNDY5 (Naimie and Lynch 1993) — a version of the linear diagnostic finite-element numerical model presented in Lynch et al. (1992). The model's horizontal mesh is the same as that on which the hydrographic fields were estimated (Fig. 2), while its vertical mesh has 21 unequally spaced nodes that lie approximately on constant $\sigma(=z/h)$ levels (where z is the vertical coordinate), with minimum spacing of 2.5 m at the surface and bottom. Linearized bottom and internal friction laws were used, with the effect of the horizontally varying current magnitude included. For the gb3 portion of the mesh, horizontally varying bottom friction coefficients and vertical eddy viscosity values were specified from a solution of the iterative nonlinear two-frequency version of the model for the M_2 tide and associated mean currents (Lynch and Naimie 1993). For the mesh extension (sns2), the friction and viscosity coefficients were specified using coefficient versus water depth relations from the eastern Scotian Shelf, inferred from the same solution. The bottom friction coefficient ranged from 0.00035 $m \cdot s^{-1}$ in deep areas to 0.003 $m \cdot s^{-1}$ on central Georges Bank, while the (vertically uniform) viscosity ranged from 0.002 to 0.1 $m^2 \cdot s^{-1}$ for the same areas.

Two sets of model solutions will be presented, with both using the condition of no normal depth-integrated flow on the land and Bay of Fundy boundaries and a geostrophic-flow condition (Lynch et al. 1992) on the downstream cross-shelf boundary. The first set (without baroclinic pressure gradients) examines the fate of barotropic inflows across the Cabot Strait (CS) and southern Newfoundland Shelf (SNS) boundaries, in order to identify pathways for the barotropic flow component and to provide guidance in the choice of boundary conditions for the subsequent baroclinic set. The barotropic inflows were obtained by specifying elevations which provide along-boundary pressure gradients on the upstream boundary of interest, with zero elevation specified on the offshore boundary. For cases with inflow specified on the SNS boundary, the geostrophic-flow boundary condition was used on the CS boundary, in order to allow the elevation difference between the SNS and CS boundaries to adjust naturally. For the case of inflow on the CS boundary, zero elevation was specified on the SNS boundary.

The second set of solutions includes forcing by the baroclinic pressure gradients associated with particular climatological density fields. The horizontal pressure gradients on the model's vertical mesh were obtained from vertical interpolation of the pressure gradients computed on the level surfaces of the optimal interpolation grid. For each season, a "regional baroclinic" solution was first obtained with "steric" conditions specified on the CS, SNS, and offshore boundaries, estimated from the density field to give no normal geostrophic flow at the seafloor. These "steric" conditions were in the form of specified elevations on the SNS and offshore boundaries, and specified depth-integrated velocities on the CS boundary (to allow natural adjustment of the elevation difference between the CS and SNS boundaries). A second "additional throughflow" baroclinic solution was then obtained for each season, with additional barotropic inflows across the SNS and CS boundaries specified based on the results of the barotropic solutions (e.g., the barotropic CS transports obtained using the geostrophic-flow boundary condition were added). These solutions are intended to illustrate the sensitivity to the uncertain barotropic inflows, and possibly provide a more realistic solution.

Hydrographic structure

The origin and general structure of water masses in the Scotian Shelf and Gulf of Maine regions have been long recognized (e.g., Bigelow 1927; Hachey 1942; McLellan 1954; Sutcliffe et al. 1976; Hopkins and Garfield 1979). Summaries of climatological temperature and salinity statistics have been available for some areas (Drinkwater and Taylor 1982; Drinkwater and Trites 1986, 1987; Petrie 1990), and there have been interpretative analyses of the structure and seasonal variation in some cases (e.g., McLellan 1954; Hopkins and Garfield 1979; Brown and Irish 1993; Petrie and Drinkwater 1993; Umoh and Thompson 1994). However, there has not been an examination of the spatial structure of the climatological hydrography extending from the southern Newfoundland Shelf to the Gulf of Maine using the recently available historical database and considering the region's pronounced topographic structure.

The basic vertical structure of the regional hydrography varies from a two-layer system in winter, when relatively cool and fresh "shelf" water overlies slope-derived water, to a three-layer system in summer when a warm surface layer develops leaving a cool intermediate layer below. As described by McLellan (1954) the combination of this vertical structure and the large differences in water depth results in strong spatial variations in the bottom water properties. In this section, we illustrate these and other broad- and topographic-scale features of the distribution of surface and bottom hydrographic properties using the climatological 3-D fields for winter and summer.

Temperature

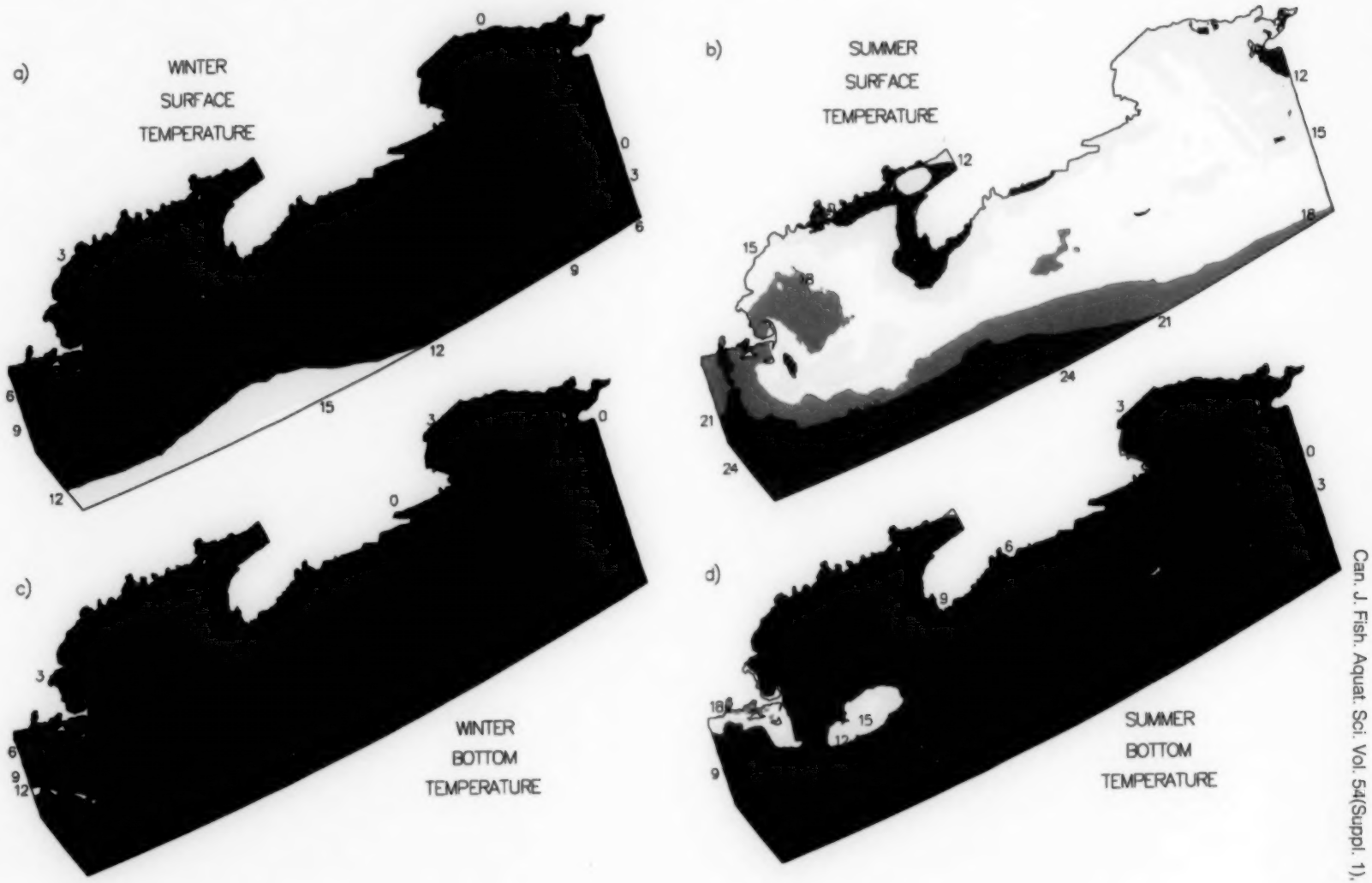
The most extensive historical hydrographic dataset exists for surface temperature which has been used in many oceanographic and biological studies (e.g., Trites et al. 1985; Koslow et al. 1987; Thompson et al. 1988). The most striking feature of the present surface temperature fields (Figs. 4*a* and 4*b*, based on bottle and CTD data only) is the large change from winter to summer, typically by about 10–14°C but exceeding 16°C in some areas (e.g., Sydney Bight). This large annual (surface) cycle is a well-documented feature of the northwestern Atlantic shelf (e.g., Weare 1977; Trites et al. 1985; Umoh and Thompson 1994), and can be attributed to the combination of continentally influenced air–sea fluxes and cold upstream sources for the shelf water.

In winter (Fig. 4*a*), cool surface water with limited spatial variability pervades the entire shelf, with temperatures less than 4°C on the Scotian Shelf and less than 6°C throughout the Gulf of Maine region. The largest spatial variations are a broad-scale increase (6–8°C) across the shelf-water/slope-water front offshore of the shelf break (e.g., Beardsley and Flagg 1976; Drinkwater et al. 1994) and weaker cross-shelf and along-shelf increases of about 3°C on the Scotian Shelf associated with subzero surface temperatures in the Cabot Strait and southern Newfoundland Shelf regions. Overall, the surface temperature pattern is consistent with along-shelf (equatorward) advection of waters from the latter two regions.

The summer surface temperature field (Fig. 4*b*) contrasts the winter field in both average value and spatial pattern. On the shelf, the largest spatial variations now occur in the Gulf

© 1997 NRC Canada

Fig. 4. Climatological mean temperature (°C) at the (*a*) surface in winter (middate of February 1), (*b*) surface in summer (middate of August 1), (*c*) bottom in winter, and (*d*) bottom in summer. Colour banding: black, <3 (with red line for the 0 contour); dark blue, 3–6; light blue, 6–9; green, 9–12; yellow, 12–15; white, 15–18; pink, 18–21; red, >21 (with black line for the 24 contour). Where water depths exceed 1000 m, bottom values are for the false bottom which slopes from 1000 to 1200 m.



© 1997 NRC Canada

of Maine region where the tidal-mixing zones off southwest Nova Scotia, in the Bay of Fundy, and over Georges Bank and Nantucket Shoals are manifested as topographic-scale zones of reduced temperature (e.g., Garrett et al. 1978). Indeed, the coolest surface temperatures in the entire domain occur off southwest Nova Scotia, consistent with the subsurface supply of cool water to this tidally energetic region (Tee et al. 1993). In contrast, spatial gradients on the Scotian Shelf are generally weaker than in winter with little evidence of along-shelf flow, but some indication of coastal upwelling (Petrie et al. 1987). Offshore, the temperature difference across the shelf-water/slope-water front is now reduced to 2–6°C depending on location.

The bottom temperature distributions (Figs. 4*c* and 4*d*) contrast the surface distributions (Figs. 4*a* and 4*b*) in having little annual variation, except in very shallow areas (e.g., nearshore; Sable Island Bank) and in the Gulf of Maine tidal-mixing zones, and in having increased topographic-scale variability over the entire shelf. The primary features of the spatial structure can be explained by the varying protrusion of the seafloor into the basic two-/three-layer vertical structure, and tidal-mixing influences on this structure (McLellan 1954).

In winter (Fig. 4*c*), bottom temperatures range from below 0°C on the southern Newfoundland Shelf to about 9°C in the deep Scotian Gulf to about 12°C at the shelf break south of Cape Cod. Two general features of the spatial structure are warmer bottom temperatures in the deep channels and basins (compared with banks) associated with the slope-derived lower layer, and warmer bank bottom temperatures in the western half of the domain (compared with the eastern half) associated with increased distance downstream and the injection of warm offshore water via cross-shelf mixing (Houghton et al. 1978).

In summer (Fig. 4*d*), the bottom temperatures on the Scotian Shelf and east are generally similar to those in winter, except in very shallow areas that penetrate the seasonal surface layer. In contrast, banks and other tidally mixed areas in the Gulf of Maine have seasonal increases in bottom temperature comparable with those at the surface, resulting in warmer summer temperatures than the adjoining basins and channels. There is a particularly stark spatial contrast in summer bottom temperature, of potential significance to fish population ranges, between the subzero values on St. Pierre Bank (southern Newfoundland Shelf) and values exceeding 12°C on Georges Bank for similar water depths. In addition to the slope-water inflows apparent in the basins and channels, the summer distribution also indicates advection over some banks: anticyclonic circulation of subzero and <9°C ("cold pool"; Houghton et al. 1982) water around St. Pierre and Georges Banks, respectively.

Salinity

The surface salinity fields for winter and summer (Figs. 5*a* and 5*b*) show broad-scale similarity, with low-salinity sources apparent in Cabot Strait and along the coast, and values generally increasing offshore across the shelf and shelf-water/slope-water front. However, there are significant annual variations with a range typically near 1 unit associated with the spring peak in freshwater discharge from major rivers (e.g., Sutcliffe et al. 1976).

In winter (Fig. 5*a*) the freshwater pulse from the St. Lawrence River discharge of the previous spring extends along the inner Scotian Shelf, with a pattern similar to that of the winter surface temperature (Fig. 4*a*). The surface salinity shows little indication of inflow from the southern Newfoundland Shelf (perhaps because the annual salinity minimum off southeastern Newfoundland occurs in early fall; Myers et al. 1990). An offshore salinity maximum is apparent in the western Gulf of Maine, however, consistent with the known deep convection in this area in winter (Brown and Beardsley 1978).

The summer surface salinity (Fig. 5*b*) clearly reflects influences of the annual cycle of river discharge. There is a well-defined freshwater plume extending from the western side of Cabot Strait to the shelf edge along Laurentian Channel and also along the inner Scotian Shelf, with indications of offshore flow off Halifax as inferred from diagnostic model solutions (Hannah et al. 1996). The strength of this signal reflects the passage of the annual salinity minimum through Cabot Strait in late summer (September; Sutcliffe et al. 1976), while there is also a hint of an additional low-salinity influence from the southern Newfoundland Shelf. In addition, significant influences from rivers discharging into the Gulf of Maine region are apparent.

In contrast with the surface distributions, the bottom salinity distributions (Figs. 5*c* and 5*d*) show little annual variation, but strongly reflect the topographic regime and the vertical salinity structure of a monotonic increase with depth below the surface. The major pathways for the penetration of Slope Water (and associated properties such as nutrients) into the shelf regime at depth are apparent: namely, Laurentian Channel into the Gulf of St. Lawrence and, through side channels, onto the southern Newfoundland Shelf; the Scotian Gulf and, to a lesser extent, the Gully (east of Sable Island) onto the Scotian Shelf; and Northeast Channel into the Gulf of Maine. These inflows provide an estuarine element to the overall shelf regime and can have significant influences on the interannual variability of water properties at all depths (Bugden 1991; Petrie and Drinkwater 1993).

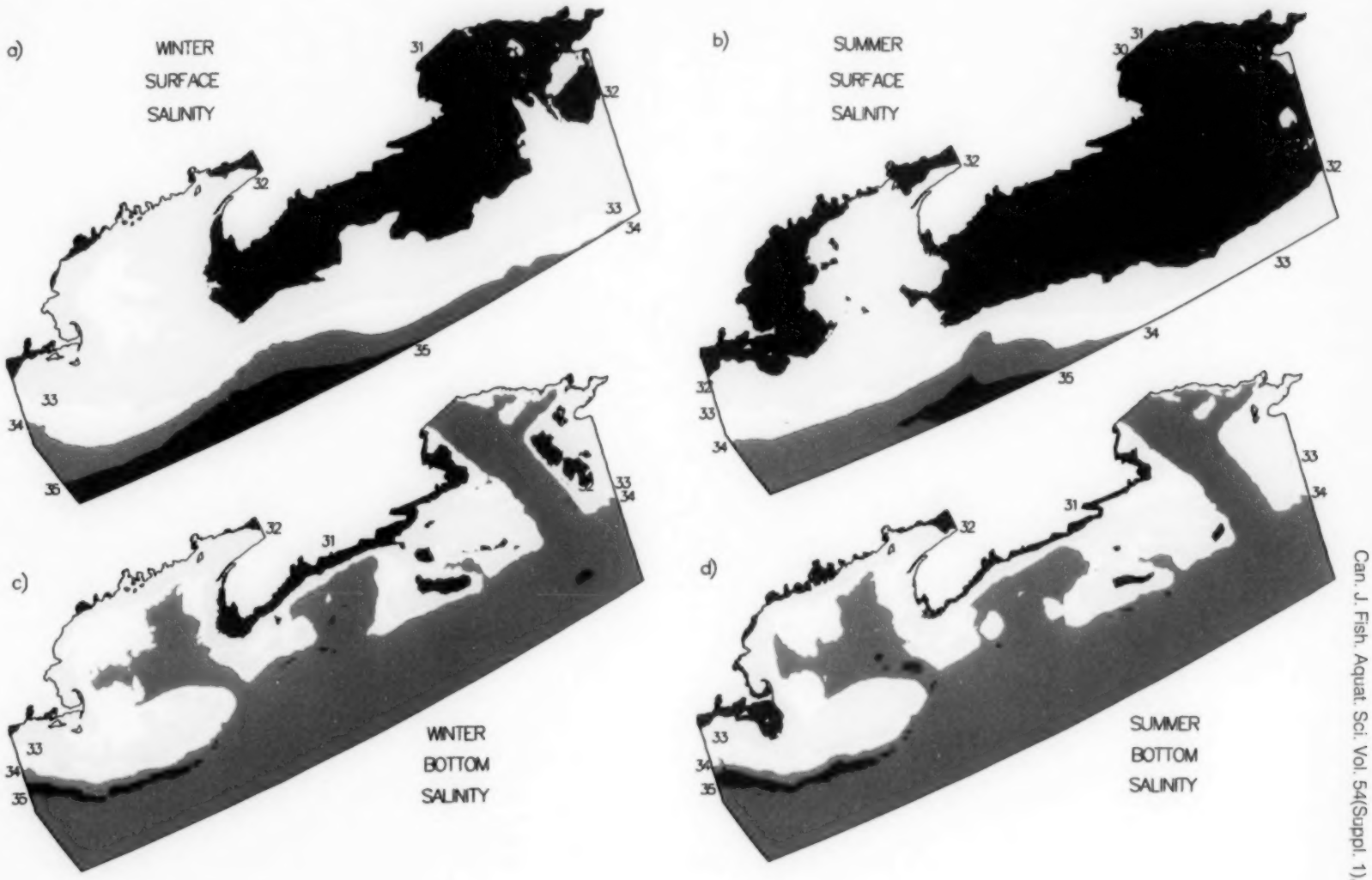
Steric height

The steric height fields provide an approximate estimate of the depth-averaged density anomaly which is indicative of the baroclinic circulation tendency at the surface in particular.

The steric fields for the present climatological cases (Fig. 6) are similar to those in the (gb3) sensitivity cases in Hannah et al. (1996, their fig. 9), with the modifications of the southern Newfoundland Shelf mesh extension and the additional anisotropy in Laurentian Channel. As described in detail by Hannah et al. (1996) for similar bimonthly fields estimated with isotropic shelf correlation scales, the fields for the gb3 domain show persistent large- and topographic-scale patterns that are generally consistent with the findings of other investigators (Csanady 1979; Csanady and Hamilton 1988; Brown and Irish 1992; Sheng and Thompson 1996) and known circulation features in the region. These patterns imply southwestward flow along the coast (with the steric high primarily associated with low-salinity coastal water), northeastward flow along the offshore boundary (with the steric high primarily associated with warm water of Gulf Stream origin), cyclonic circulation in the Slope Water (including southwest-

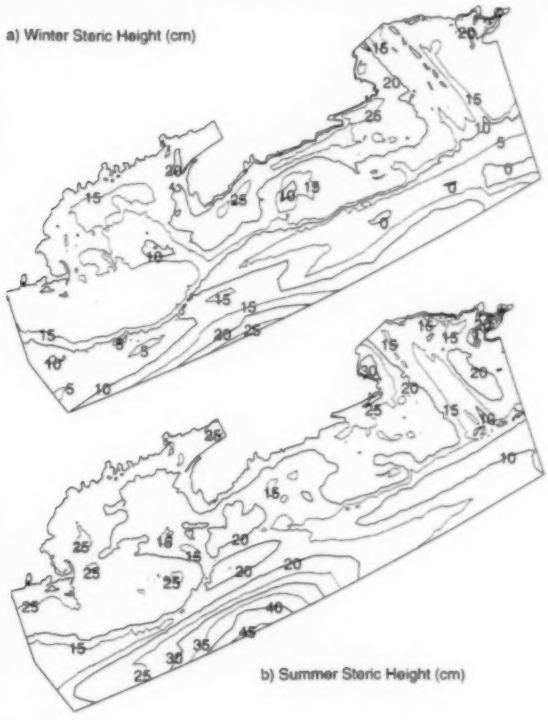
© 1997 NRC Canada

Fig. 5. Climatological mean salinity at the (*a*) surface in winter, (*b*) surface in summer, (*c*) bottom in winter, and (*d*) bottom in summer. Colour banding: dark blue, <30; light blue, 30–31; green, 31–32; yellow, 32–33; white, 33–34; pink, 34–35; red, >35. Where water depths exceed 1000 m, bottom values are for the false bottom which slopes from 1000 to 1200 m.



© 1997 NRC Canada

Fig. 6. Steric height relative to 1200 m in (*a*) winter and (*b*) summer. A constant has been subtracted from all values.



ward flow near the 1000-m isobath, as found by Csanady 1979), and cyclonic (anticyclonic) circulation over basins (banks) on the shelf. These features are also present in the Laurentian Channel and southern Newfoundland Shelf regions (Fig. 6), although there are indications that the steric setup on the inner Scotian Shelf receives a greater contribution from flow through Cabot Strait than from the southern Newfoundland Shelf and that the cyclonic circulation tendency over Laurentian Channel is either less pronounced or more poorly resolved (because of data sparsity) than over other deep areas on the shelf.

Seasonally, the steric height generally increases by 5–10 cm between winter and summer, consistent with thermal expansion associated with surface heating. Exceptions to this occur on the inner Scotian Shelf where there is an offsetting contribution from the low-salinity Cabot Strait flow which increases the steric heights in winter, and in the vicinity of the offshore boundary off Georges Bank where the summer increase is larger than elsewhere. The latter is qualitatively consistent with the northward shift in the positions of the shelf-water/slope-water front and Gulf Stream during summer–fall found by Drinkwater et al. (1994), although the structure of this feature in the present fields is suspect because of data sparsity in this highly variable region. For the same reason, the reliability of the seasonal and spatial structure of the baroclinic circulation tendency in the Slope Water is uncertain, although there is a clear suggestion that the southwestward upper-slope current turns offshore off the western Scotian Shelf, with greater westward penetration and transport in winter (also see Hannah et al. 1996). These features indicate that the low-salinity flow from the Gulf of St. Lawrence is an important contributor to the phase shift of the seasonal cycle of coastal sea level between the Scotian Shelf (Halifax, Yarmouth) and the Gulf of Maine (Portland, Boston) found by Thompson (1986, his table 1), in addition to a possible contribution from the seasonal variation in Slope Water circulation.

Circulation model results

Background

The seasonal-mean circulation in the greater Scotian Shelf region is generally considered to be a continuation of a large-scale "coastal" current on the northwestern Atlantic shelf, supplemented by flow from the Gulf of St. Lawrence (e.g., Smith et al. 1978; Chapman and Beardsley 1989; Loder et al. 1996). However, in the outer Laurentian Channel region where these currents meet in the presence of rugged bathymetry, only limited observational information and numerical model guidance are available regarding the flow patterns: current and hydrographic property descriptions across Cabot Strait (e.g., El Sabh 1977), sea surface slope estimates from satellite altimetry (Han et al. 1993), and barotropic model solutions for the Newfoundland Shelf (Greenberg and Petrie 1988).

Literature values for the net (cross-sectional average) monthly- or seasonal-mean transport through Cabot Strait are typically of order 0.01 Sv (e.g., El Sabh 1977), essentially the value of the freshwater discharge into the Gulf of St. Lawrence. However, recent observations (Petrie et al. 1988) that the transport into the Gulf through the Strait of Belle Isle has a mean summer value of 0.13 Sv and a mean winter value of 0.3 Sv suggest that net seasonal-mean transports of 0.1–0.3 Sv through Cabot Strait are plausible. While the net Cabot Strait transports are uncertain, it is known that the inflow (to the model) on the Strait's western side and outflow (from the model) on its eastern side can substantially exceed the net value. Typical monthly-mean values for these flows are in the range 0.3–1.0 Sv (Lawrence 1968; El Sabh 1977; Sutcliffe et al. 1976; Bugden 1981), with peak seasonal inflow (to the model) in early fall, although there appears to be significant variability about the climatological annual cycle. (Note that our convention of referring to the Cabot Strait flows as in/outflows relative to the model domain differs from the customary usage of out/inflows relative to the Gulf of St. Lawrence.)

The magnitude and structure of the inflow along the Newfoundland Shelf are less clear. Firm information is available for the northern Grand Bank region (e.g., Petrie and Anderson 1983; Greenberg and Petrie 1988), indicating that an inshore branch of the Labrador Current flows around the Avalon Peninsula with a transport of 0.4–0.6 Sv and an offshore branch flows along the eastern Bank edge with a transport of 4–10 Sv. However, the fate of these flows in the southern Newfoundland Shelf region is somewhat uncertain, except for indications that only a fraction of the offshore branch continues around the Tail of the Bank (e.g., Clarke et al. 1980) and that there is further offshore loss to the Slope Water off the southwestern Grand Bank (Csanady and Hamilton 1988). Satellite altimetry (Han et al. 1993) indicates a synchronous annual variation in cross-shelf elevation slope over the shelf

© 1997 NRC Canada

Table 1. Summary of transports (in units of Sv) across key sections in the barotropic model cases.

Case	Fig.	SNS-I	SNS-SB	CS-W	CS-E	Halfx	SWNS	NanSh
Base components								
SNS-I inflow	7*b*	0.52	0.07	0	–0.48	0	0	0
SNS-SB inflow	7*c*	0.03	0.93	0	–0.48	0.04	0.04	0.03
CS inflow: narrow	7*d*	0	0	0.50	0	0.23	0.16	0.06
Sensitivity case								
CS inflow: broad	7*e*	0	0	0.50	0	0.09	0.07	0.03
CS inflow: friction	7*f*	0	0	0.50	0	0.17	0.09	0.03
Composites								
Base case	8*a*	0.29	0.50	0.52	–0.52	0.25	0.18	0.07
Alternative	8*b*	0.28	0.50	0.48	–0.48	0.11	0.10	0.04

Note: The cases are presented in the same order as the streamfunction plots in Figs. 7 and 8 (panels indicated in second column). The sections are indicated and their acronyms defined in Fig. 1. Positive transports are into the model or along-shelf towards the southwest.

breaks off Laurentian Channel and the southwestern Grand Bank with peak along-shelf flow in winter, while barotropic model simulations (Greenberg and Petrie 1988) suggest that about 50% of the transport around the tail of the Grand Bank reaches the Laurentian Channel region.

Barotropic inflows

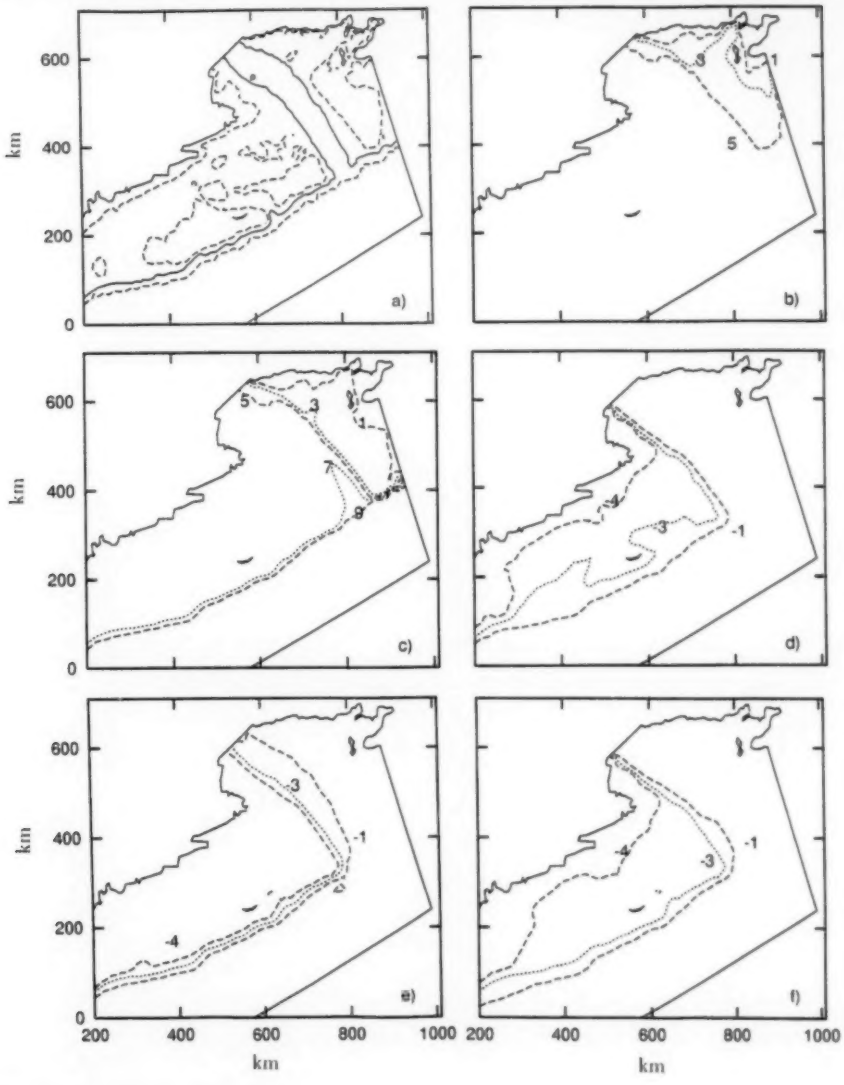
We start our model investigation with an examination of the barotropic pathways for inflows across the CS and SNS boundaries and of the interrelation of flows across these boundaries (e.g., SNS inflow supplying CS outflow). In view of the available observational information, we consider inflows on three specific boundary segments (Fig. 1): the inner portion (74 km) of the SNS boundary, as a potential location for the inshore branch of the Labrador Current; the shelf-break region (150 m $\leq h \leq$ 720 m) of the SNS, as the probable location of the offshore Labrador Current; and the two westernmost elements on the CS boundary (henceforth, "narrow" CS inflow), out to the model node where h = 181 m (effectively, west of St. Paul Island). In each case, we specify a linear elevation gradient along the segment such that the incoming velocity is approximately uniform (subject to dynamical adjustments in the model) and hence the local transport is proportional to water depth. For the CS inflow case, a nominal transport of 0.5 Sv is used, while the transport inflow for each SNS case is chosen to yield an outflow of approximately 0.5 Sv across the CS boundary (where the geostrophic-flow boundary condition allows a natural adjustment in both the structure and mean value of the elevation). The net transports across key sections in various parts of the model domain (Fig. 1) are summarized in Table 1 for these and other barotropic (i.e. without baroclinic pressure gradients) model solutions.

The flow patterns in the eastern Scotian Shelf region associated with these basic boundary forcings, displayed using the (vertically integrated) transport streamfunction (Figs. 7*b*–7*d*), show strong similarity to the local isobaths (Fig. 7*a*) that dominate the regional geostrophic (f/h) contours (where f is the Coriolis parameter). All of the inner SNS inflow (of about 0.5 Sv) leaves the model domain on the eastern side of Cabot Strait (Fig. 7*b*), with the nearshore portion generally moving along the coast and the offshore portion moving around St. Pierre Bank. In contrast, only about half of the shelf-break SNS inflow (of 1 Sv) leaves across the CS boundary (Fig. 7*c*; Table 1), with the remainder (the offshore portion) moving along the outer Scotian Shelf either directly or after an excursion into the Laurentian Channel. Alternatively viewed, most of SNS barotropic inflow inside the 200-m isobath moves into the Gulf of St. Lawrence, while that offshore of this isobath moves along the Scotian Shelf break. The partitioning of the inflows is sensitive, however, to their specified distribution on the incoming geostrophic contours and to the bottom stress magnitudes (see below).

Even with the narrow CS inflow concentrated near the Cape Breton coast (Fig. 7*d*), most of the transport moves along the western edge of Laurentian Channel and then the Scotian Shelf break, with only about one third of the transport moving onto the inner Scotian Shelf and none moving to the southern Newfoundland Shelf (Table 1). The exact fraction of the CS inflow that moves onto the inner Scotian Shelf is, however, dependent on both the cross-channel structure of the CS inflow and the bottom stress magnitudes. These dependencies are illustrated (Table 1) by sensitivity cases with the CS inflow redistributed out to the deepest channel node where h = 467 m ("broad" CS inflow; Fig. 7*e*), and with the bottom friction and viscosity coefficients increased by a factor of 4 (Fig. 7*f*). In both cases there is reduced flow onto the inner Shelf, pointing to the general conclusion that the primary barotropic pathway for CS inflow is along the outer Scotian Shelf break. These results are consistent with the known underlying physics of frictional barotropic flow (e.g., Csanady 1978; Wright et al. 1986; Lynch et al. 1992): namely, that the velocity field is essentially geostrophic flow with bottom Ekman layers, so that the flow patterns are entirely determined by the specification of transport on geostrophic contours at the model boundaries and by the bottom stress magnitudes. The redistribution of the CS inflow offshore (inshore) onto deeper (shallower) geostrophic contours results in less (more) flow on the inner Scotian Shelf. Similarly, increased bottom stress magnitudes (through increases in either the bottom friction coefficients or the near-bottom eddy viscosities;

© 1997 NRC Canada

Fig. 7. Transport streamfunction in the eastern Scotian Shelf region for (*b*) inner SNS inflow, (*c*) shelf-break SNS inflow, (*d*) narrow CS inflow, (*e*) broad CS inflow, and (*f*) narrow CS inflow with bottom friction and viscosity coefficients increased by a factor of 4. The base-case friction and viscosity coefficients derived from the nonlinear M_2 tidal solution are used in Figs. 7*b*–7*e*. The streamlines are labelled in units of 10^5 $m^3 \cdot s^{-1}$. The streamfunction value is zero on the Newfoundland coast, and low values are on the right looking downstream (opposite to the convention used by some). (*a*) Regional bathymetry using the 100-, 400-, and 1000-m isobaths. Coordinates are the same as in Fig. 1.



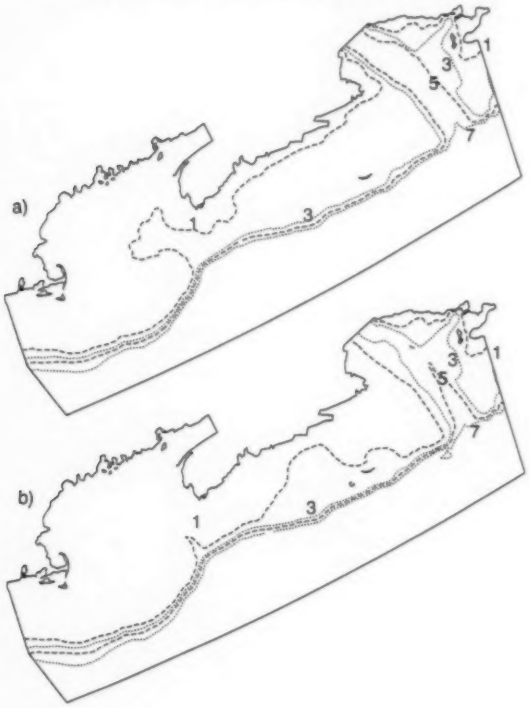
Greenberg et al. 1996) result in more offshore transport in the bottom Ekman layer and hence more offshore "diffusion" of the depth-integrated transport (Csanady 1978). This effect also applies to the SNS inflows, resulting in smaller fractions of the inflows leaving through Cabot Strait when bottom stress magnitudes are increased.

The broad CS inflow case (Fig. 7e) also reveals a significant small-scale topographic influence in Cabot Strait: the model boundary is on the seaward edge of a topographic depression (amplitude about 100 m and horizontal scale about 40 km). As a result, the deeper geostrophic contours on the CS boundary are locally closed, providing a local recirculation pathway (CS inflow on the western side supplying CS outflow on the eastern side). With zero elevation gradient specified on the eastern CS boundary in the present case (retarding outflow), the depression diverts the deep-water fraction of the inflow across the Channel (Fig. 7*e*). Moored current measurements (Lawrence 1968) indicate that the near-bottom midstrait flows are largely directed northeastward across the Channel, providing support for a significant topographic "trapping" influence on the flow through Cabot Strait.

The net effects of these inflows and their influences further downstream are illustrated by composites of the above solu-

© 1997 NRC Canada

Fig. 8. Transport streamfunction over the entire ss2 model domain for (*a*) the "base" composite barotropic case taken as the combination of narrow CS inflow (Fig. 7*d*) and inflows on the inner and shelf-break SNS boundaries (one half of those in Figs. 7*b* and 7*c*) and (*b*) the combination of broad CS inflow (Fig. 7*e*) and the same inflows on the inner and shelf-break SNS as in Fig. 8*a*. Base-case friction and viscosity coefficients from the nonlinear M_2 tidal solution are used in both cases. The streamlines are labelled in units of 10^5 $m^3 \cdot s^{-1}$. The streamfunction value is zero on the Nova Scotia and U.S. coasts, and low values are on the right looking downstream.



tions (Fig. 8; Table 1), obtained through linear superposition of the individual-inflow boundary conditions. For use in the baroclinic solutions (below), a base composite barotropic case is chosen (Fig. 8*a*) as the combination of the narrow CS inflow (Fig. 7*d*) and of inflows on the inner and shelf-break SNS boundaries such that the outflow on the eastern CS boundary receives equal contributions from the two SNS inflows (requiring half of the transports in Figs. 7*b* and 7*c*). To illustrate the sensitivity of the net flow, an alternative composite case is also shown (Fig. 8*b*) using the broad CS inflow (Fig. 7*e*). The linear dynamics in these solutions are expected to be a valid first approximation for the barotropic flow, although recent studies suggest an important barotropic–baroclinic coupling through the bottom boundary layer (e.g., Gawarkiewicz and Chapman 1992; Greatbatch and Goulding 1992).

As expected, the base composite solution (Fig. 8*a*) shows most of the shelf-break SNS inflow continuing along the shelf break and upper slope of the Scotian Shelf and Gulf of Maine (some after an excursion into the Laurentian Channel). The inner SNS inflow and part of the shelf-break SNS inflow leave the model on the eastern side of Cabot Strait, with a corresponding inflow on the Strait's western side that further supplies the Scotian Shelf break flow as well as the small inner Shelf flow. In the Gulf of Maine, there is weak cyclonic (anticyclonic) flow around the deep (shallow) basins (banks), with only about one third of the inflow inside the 200-m isobath on the SNS and CS boundaries remaining on the shelf (neglecting barotropic–baroclinic coupling). This fraction increases (decreases) with decreases (increases) in the bottom friction coefficients and/or near-bottom eddy viscosities.

The most notable feature of the alternative composite case with broad CS inflow (Fig. 8*b*) is that a smaller fraction of the SNS inflow leaves across the CS boundary, with some flow apparently turned back in the outer Laurentian Channel. This effect is similar to that described by Wang (1982) and Chapman et al. (1986) whereby along-shelf (barotropic) flow over the continental slope apparently prevents shelf flow from moving offshore. Considering the linear dynamics in these studies, this apparent flow interaction can also be interpreted as the result of offsetting contributions from linear flow components, with part of the CS inflow offsetting the SNS inflow moving toward the CS boundary, and the offshore loss of along-shelf flow on the shelf being offset by the onshore diffusion of along-shelf flow over the slope.

Baroclinic circulation strategy

The bimonthly baroclinic solutions on a coarser mesh (g2s) and the winter and summer sensitivity cases on the gb3 mesh in Hannah et al. (1996) clearly demonstrate the occurrence of important baroclinic circulation in the greater Scotian Shelf region, with both year-round persistence in pattern and seasonal changes in strength. Those solutions used "steric" elevations (giving zero normal geostrophic bottom flow) on a single upstream boundary across Cabot Strait and along the Laurentian Channel, but several aspects of the upstream boundary conditions were identified to require further investigation. The extended mesh and density fields presented here for winter and summer allow examination of these issues, as well as consideration of the baroclinic circulation in the Laurentian Channel and southern Newfoundland Shelf regions.

As described earlier, "regional baroclinic" solutions are first obtained for each season with baroclinic pressure gradient forcing and "steric" conditions specified on the two upstream boundary segments (CS and SNS). These solutions should provide (subject to density data adequacy) physically plausible flow fields for the influence of the baroclinic pressure field within the model and on its boundaries. However, they may not represent the full influence of baroclinicity because of the neglect of density evolution and barotropic flows (of baroclinic origin; e.g., Shaw and Csanady 1983; Weaver and Hsieh 1987) from upstream, nor the complete circulation because of the neglect of other forcings (wind, tides). Consequently, "additional throughflow" baroclinic solutions are also presented, obtained by adding 50% of the base composite barotropic solutions (Fig. 8*a*) to the regional baroclinic solutions. To aid the evaluation and intercomparison of various flow fields, in relation to both the Hannah et al. (1996) solutions and observations, we show in Table 2 the transports across the key sections (Fig. 1).

© 1997 NRC Canada

Table 2. Summary of transports (in units of Sv) across key sections in the baroclinic model solutions.

Case	SNS-I	SNS-SB	CS-W	CS-E	Halfx	SWNS	NanSh
Summer							
Regional baroclinic	–0.08	0.18	0.58	–0.50	0.39	0.15	0.42
Additional throughflow	0.06	0.42	0.82	–0.73	0.50	0.23	0.46
Hannah et al. 1996 (gb3)	—	—	—	—	0.62	0.33	0.40
Increased friction	–0.08	0.14	0.57	–0.40	0.45	0.09	0.30
Laurentian Channel	–0.13	0.14	0.38	–0.09	0.37	0.13	0.42
Increased anisotropy	–0.07	0.14	0.34	–0.15	0.40	0.14	0.41
Midtime: August 21	–0.02	0.52	0.22	–0.12	0.27	0.25	0.34
Winter							
Regional baroclinic	0.01	0.14	0.81	–0.54	0.92	0.33	0.33
Additional throughflow	0.15	0.36	1.1	–0.77	1.0	0.42	0.36
Hannah et al. 1996 (gb3)	—	—	—	—	1.1	0.48	0.35
Laurentian Channel	0.00	0.14	0.48	–0.29	0.90	0.32	0.22
Midtime: March 1	0.04	0.50	0.53	–0.34	0.78	0.50	0.38

Note: The sections, indicated in Fig. 1, are the same as those in Table 1. Positive transports are inflows or southwestward. The regional baroclinic and additional throughflow cases are alternative base cases. The Hannah et al. (1996) (gb3) cases correspond to fig. 10 in Hannah et al. (1996). The other (sensitivity) cases are for the regional baroclinic circulation without additional throughflow: the increased friction case has friction coefficients increased by a factor of 4; the Laurentian Channel cases have no additional anisotropy there beyond the shelf-wide topographic anisotropy; the increased anisotropy case has $b_a = 15$, with no additional anisotropy in the Laurentian Channel; and the alternative midtime cases have no additional anisotropy in the Laurentian Channel.

Summer

We first present the results for summer which has a stronger steric signal in the Laurentian Channel region and for which the model circulation patterns there are more physically plausible (than for winter). The overall spatial pattern of the "regional baroclinic" transport field (Fig. 9*a*) closely resembles that in the corresponding summer gb3 solution in Hannah et al. (1996, their fig. 10*b*), but the along-shelf transport magnitudes are significantly reduced: by over 0.2 Sv on the Halifax section and about 0.1 Sv in the Gulf of Maine (Table 2). These differences can be traced to the Laurentian Channel region where the present solution has reduced inflow through Cabot Strait and reduced trapping of the flow along the western edge of the Laurentian Channel. This further illustrates the sensitivity to upstream boundary conditions and indicates that the Laurentian Channel boundary location on the earlier grids (g2s, gb3) may artificially restrict the off-shelf diffusion of the CS inflow.

The regional baroclinic solution (Fig. 9*a*) indicates that the primary upstream baroclinic pathway for the supply of shelf water to the greater Scotian Shelf region in summer is flow out of the Gulf of St. Lawrence on the western side of Cabot Strait, with local transports exceeding 0.5 Sv but only about 0.3 Sv reaching the shelf-break region. Much of this flow recirculates cyclonically over the Laurentian Channel, but there is some indication of an interconnection with cyclonic circulations over the eastern Scotian Slope and shelf basins downstream. However, there are a number of small-scale flow features of questionable reliability (e.g., possible artifacts of aliased temporal variations in the density field) which may be affecting the continuity of streamlines, as in diagnostic solutions in general (Hannah et al. 1996). In contrast, there is little baroclinic transport across the shelf portion of the SNS boundary or on the southern Newfoundland Shelf proper. Together with the hydrographic and steric fields (e.g., Figs. 5*b* and 6*b*), this solution indicates that the freshwater plume from the Gulf of St. Lawrence is the primary forcing of baroclinic circulation on the eastern Scotian Shelf in summer and that the largest associated transports are in deep areas such as the Laurentian Channel and possibly the Scotian Slope. Nevertheless, the hydrography and the model velocity field (not shown) indicate an associated current branch on the inner Scotian Shelf, but with only a small transport (0.12 Sv between the coast and Banquereau Bank).

The net CS flow of 0.08 Sv (into the model) and the inflow of 0.58 Sv on the Strait's western side in the regional baroclinic solution (Table 2) are in the general range of the observational estimates noted above. This suggests that the solution is a plausible realization of the summer baroclinic regime in the vicinity of the CS boundary. However, considering observational uncertainties in the barotropic flow through Cabot Strait (or equivalently, the level of no motion) and indications of substantial barotropic flow in the Labrador Current on the Newfoundland Shelf, additional barotropic throughflows in the Scotian Shelf region cannot be ruled out.

The "additional throughflow" solution (Fig. 9b) provides an indication of the net effects of local baroclinicity and barotropic throughflow. The additional outflow of 0.23 Sv on the eastern CS boundary requires additional inflows of 0.14 and 0.24 Sv across the inner and shelf-break SNS segments under the presently assumed inflow partitioning (Table 2). The associated shelf-slope flows and those resulting from the additional inflow of 0.24 Sv on the western CS boundary generally reinforce the baroclinic circulation and enhance the weak flow on the inner Scotian and southern Newfoundland shelves. Some reduction in the relative importance of local baroclinic flow structures is apparent in the Laurentian Channel and along the Scotian Shelf break, resulting in increased

© 1997 NRC Canada

Fig. 9. Summer transport streamfunction (10^5 $m^3 \cdot s^{-1}$) for (*a*) the regional baroclinic solution (with steric upstream boundary conditions) and (*b*) the additional throughflow baroclinic solution (one half of the flow field in Fig. 8*b* added to that in Fig. 9*a*). The streamfunction value is zero on the Nova Scotia and U.S. coasts, and low values are on the right looking downstream. The streamfunction value on the Newfoundland coast is indicated.

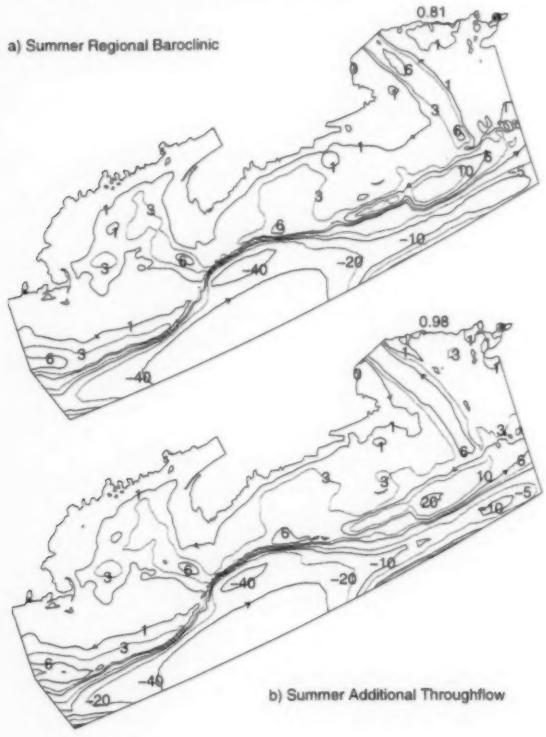
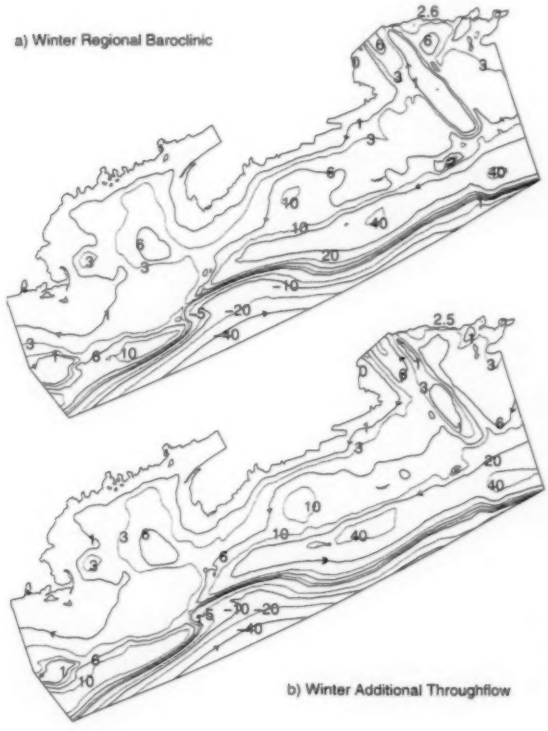


Fig. 10. Winter transport streamfunction (10^5 $m^3 \cdot s^{-1}$) for (*a*) the regional baroclinic solution and (*b*) the additional throughflow baroclinic case. The presentation format is the same as for Fig. 9.



continuity of the streamlines, but the effects are small in the Gulf of Maine region.

Comparison of the transports in these solutions (Table 2) with the observed summer transports from moored measurements on the southwestern Nova Scotia (<0.1 Sv; Smith 1983) and Nantucket Shoals (0.39 Sv; Ramp et al. 1988) sections points to little (if any) need for additional upstream inflow. Comparison with the geostrophic transport of about 0.2 Sv on the Halifax section in summer estimated by Drinkwater et al. (1979) indicates that the actual level of no motion is deeper than the 100 m assumed in their estimate, and that there are substantial nonzero bottom velocities in places (indicating that significant barotropic flows are generated within the model domain). While these comparisons suggest that the regional baroclinic solution is more realistic than the additional throughflow solution, they do not preclude additional barotropic inflow from the Newfoundland Shelf provided that it is offshore of the 200-m isobath. (Further investigation of the fate of such inflow is not pursued here because it is influenced by the deep-ocean false bottom.)

Winter

On the Scotian Shelf and in the Gulf of Maine, both the regional baroclinic and additional throughflow transport fields for winter (Fig. 10) have patterns and strength similar to those in the winter cases in Hannah et al. (1996). This supports the overall robustness of the various winter solutions and the importance of baroclinic circulation to the seasonal-mean circulation and points to limited sensitivity of the downstream flow to upstream boundary conditions. However, as in summer, the downstream transports in the present regional baroclinic solution are about 20% smaller than in the corresponding gb3 winter case (Table 2), consistent with the (small) trapping influence suggested earlier for the gb3 Laurentian Channel boundary. Note that this influence appears to be greater than the influence of the additional throughflow in the present solutions.

The regional baroclinic solution shows the expected inflow/outflow pattern on the western/eastern sides of the CS boundary and weak inflows on the SNS boundary segments (Fig. 10*a*; Table 2). About 0.28 Sv of the CS inflow moves onto the inner Scotian Shelf (inside Banquereau Bank), suggesting a year-round Gulf of St. Lawrence influence on the eastern Scotian Shelf. However, most of the CS in/outflows are part of a cyclonic half-gyre near the boundary, and the overall Laurentian Channel circulation is dominated by an elongated anticyclonic cell with currents directed opposite to the barotropic pathways (Fig. 7) along the Channel's sides (assuming barotropic inflows on the SNS and western CS boundaries). Some indication of this cell is apparent in the

© 1997 NRC Canada

winter steric field (Fig. 6*a*), but the reliability of the climatological density field in this region is unclear in view of data sparsity. On the other hand, both the cyclonic half-gyre on the CS boundary and the anticyclonic Laurentian Channel cell overlie topographic depressions, supporting the possibility of topographic trapping. The SNS inflows are apparently blocked by the Laurentian Channel cell and move onto the Scotian Shelf, so that there is little interconnection between the SNS and CS boundary flows in the winter solutions, even in the additional throughflow case (Fig. 10*b*). Further offshore over the southern Newfoundland slope, there is significant inflow which moves along the Scotian Shelf break as part of an intensified cyclonic slope gyre and eventually feeds the cyclonic circulation over Emerald Basin. The winter intensification of this flow is consistent with the bimonthly solutions in Hannah et al. (1996) and Han et al.'s (1993) observations, but data sparsity is also a general problem over the slope, limiting the reliability of the model solutions for the slope and deep ocean.

Finally, comparison of the winter transports (Table 2) with moored measurements on the Halifax (1.0 Sv; Anderson and Smith 1989), southwestern Nova Scotia (0.3 Sv; Smith 1983), and Nantucket Shoals (0.4 Sv; Ramp et al. 1988) sections indicates approximate agreement for both the regional baroclinic and additional throughflow solutions, with slightly better agreement for the latter. This suggests again that the overall (shelf) flow patterns are generally robust and realistic, with transport uncertainties of only about 20% associated with the upstream boundary details. However, as in summer, additional barotropic throughflow over the continental slope cannot be ruled out.

Sensitivity of baroclinic circulation

Table 2 also indicates the sensitivity of the regional baroclinic solutions to four factors involving somewhat arbitrary choices in the diagnostic model application: (*i*) the magnitude of the bottom friction and eddy viscosity coefficients, (*ii*) the additional anisotropy specified in the horizontal correlation scales in the Laurentian Channel, (*iii*) the shelf-wide topographic anisotropy in the horizontal correlation scales, and (*iv*) the choice of season midtime. For summer, sensitivity cases are shown for all four factors, while for winter, cases are shown for Laurentian Channel anisotropy and midtime (the expected leading sensitivity factors in the Laurentian Channel region).

The summer solution with friction and viscosity coefficients increased fourfold shows the expected downstream influence of reduced transports in the Gulf of Maine region, consistent with the (weak) frictional dynamics discussed above. An interesting exception to this is a local transport increase on the Halifax section, indicating that the frictional redistribution of transport on geostrophic contours in the baroclinic case can have local effects which differ qualitatively from those on the barotropic flow (Figs. 7*d* and 7*f*; Table 1).

The three density-field factors (*ii–iv*) show no major qualitative influences on the shelf circulation, but some significant quantitative influences, particularly in the Laurentian Channel region. Elimination of the additional anisotropy in the Laurentian Channel results in substantial reductions in the flow magnitudes across the CS boundary and changes in the flow details in the Channel in both seasons, but limited influences downstream. Increasing the shelf-wide topographic anisotropy results in a slight increase in the continuity of streamlines in some areas (consistent with the findings of Hannah et al. 1996), but no significant change in the section transports. The alternative midtimes result in significant changes in some local flow features in various parts of the study domain, but no qualitative change in the major features of the shelf regime.

Collectively, the diagnostic solutions presented here together with those in Naimie et al. (1994) and Hannah et al. (1996) point to the following general conclusions: (1) the historical density database in the western Scotian Shelf and Gulf of Maine regions appears adequate for a diagnostic evaluation of the major features of the seasonal baroclinic (shelf) flow fields, (2) the historical density database in the eastern Scotian Shelf and southern Newfoundland Shelf regions is marginal for the diagnosis of seasonal circulation, yielding plausible circulation fields in summer but questionable ones in winter, (3) significant information on upstream influences (e.g., from the eastern Scotian Shelf region) can be stored in local density fields (e.g., the Gulf of Maine region) such that, when the barotropic flow component is secondary, diagnostic model flow fields can have limited sensitivity to details of the upstream regime, in spite of significant dynamical influences, and (4) in view of the difficulty of reliably extracting the mean spatial structure in a temporally variable density field, the critical evaluation of diagnostic flow fields should involve the examination of dynamical plausibility and observational realism, as well as sensitivity to various factors.

While the overall results of our studies to date demonstrate the value of diagnostic models in quantifying the seasonal baroclinic circulation, and conclusion (3) points to a possible advantage of diagnostic solutions, our results nevertheless support the clear need to allow some degree of density field evolution in baroclinic circulation studies. In this context, many of the issues of density field estimation and boundary condition sensitivity discussed here become part of the initialization and boundary-condition strategy for prognostic circulation models.

Discussion

The above view of the climatological hydrography and circulation in the Scotian Shelf and Gulf of Maine regions demonstrates their pronounced spatial and temporal variability, the wealth of information in historical datasets, and the promise of 3-D circulation models for integrating historical data and for interpreting regional study results on realistic large-scale geometry.

Many known features of the annual, vertical, cross-shelf, and along-shelf variations of hydrography on the northwestern Atlantic shelf are apparent in the surface and bottom fields (Figs. 4 and 5). Those that have received only limited attention include (*i*) the large along-shelf variation in bottom temperature between the southern Newfoundland Shelf and the Gulf of Maine region, (*ii*) the contrasting magnitudes and phases of the annual bottom temperature variations over submarine banks and adjacent basins (Georges Bank versus Georges Basin), (*iii*) the increased depth of penetration of the

© 1997 NRC Canada

annual temperature variation in the tidally energetic Gulf of Maine region, (*iv*) the pronounced directional asymmetry in (near-surface) low-salinity Gulf of St. Lawrence water moving onto the open shelf, with primary pathways onto the inner and outer (along the shelf break) Scotian Shelf, and (*v*) the importance of a few deep channels in providing conduits for the movement of Slope Water, and associated nutrients and other water-mass properties, onto the shelf.

While the hydrographic distributions are consistent with the conventional wisdom of along-shelf flow with most of the Scotia–Maine shelf water originating upstream (Gulf of St. Lawrence and/or Newfoundland Shelf), the distributions also point to significant regional regimes. These include: the southern Newfoundland Shelf, presumably strongly influenced by the upstream Newfoundland Shelf; the eastern Scotian Shelf, with influences from both the Gulf of St. Lawrence (inner and outer shelf) and the southern Newfoundland Shelf (along the shelf break); the western Scotian Shelf, a transition region with moderate Slope Water influences; and the Gulf of Maine region, strongly influenced by tidal mixing and Slope Water inflow. This gradual termination of the subpolar western boundary current influence provides an interesting and potentially sensitive climatological setting for various bank- and basin-scale habitats.

The diagnostic model results presented here and in Hannah et al. (1996) provide a first quantitative description of the associated baroclinic flow field that generally dominates the seasonal-mean circulation. This description complements the hydrographic fields in identifying large-scale, regional, and topographic-scale (banks, basins) features of the physical oceanographic regime. Partial large-scale throughflow with seasonal variability is confirmed by the present solutions, although the exact fraction is dependent on unresolved local flow features. Strong tendencies for anticyclonic (cyclonic) baroclinic circulation over banks (basins) are indicated by the steric height and transport fields. Together with the deep channels and coastline indentations that are major conduits for cross-shelf flow, the banks and basins also contribute to the different regional regimes. Connections between the southern Newfoundland and Scotian shelves vary seasonally, with the present solutions indicating year-round flow along the shelf break and an additional indirect route via the Gulf of St. Lawrence in summer. Transport of water from the Gulf of St. Lawrence onto the Scotian Shelf occurs year-round with an annual variation in properties (and probably strength). Further downstream, the cyclonic flow around Emerald Basin plays an important role in connecting the eastern and western Scotian shelves, while there appears to be a partial bottleneck in the along-shelf flow off southwestern Nova Scotia (Hannah et al. 1996).

On the other hand, the model solutions also indicate expected limitations in the applicability of diagnostic circulation models to areas with limited historical data coverage (relative to spatial and temporal density variations). Various suspicious small-scale flow features and the anticyclonic winter circulation cell over the Laurentian Channel require further dynamical and/or observational investigation. From both hydrographic and circulation perspectives, data sparsity is particularly severe in the shelf regime "junction" in the Laurentian Channel region, and along much of the shelf break. Nevertheless, the hydrographic and initial circulation fields presented here demonstrate the potential of the historical database and diagnostic circulation models, particularly if complemented by further retrieval of historical data, further data collection in key areas, increasingly sophisticated optimal interpolation procedures, dynamical diagnostics, and prognostic models for evolving the hydrographic fields into dynamical consistency.

Acknowledgements

We are grateful to the many individuals who have contributed to the historical hydrographic database, the FUNDY5 circulation model, and our analyses. We extend special thanks to Ken Drinkwater and Roger Pettipas for their lead role in the database assembly, Ian He, Gerry Boudreau, and Ross Hendry for providing the optimal interpolation program, Dan Lynch and Chris Naimie for providing the numerical model and related algorithms, as well as ongoing advice on their implementation, Mary Jo Graça for invaluable assistance in the hydrographic field computations and in the preparation of field displays, Brian Petrie for ongoing observational advice, and Jinyu Sheng, Keith Thompson, and Dan Wright for theoretical advice. This work has been jointly funded by the Interim Funding Research Program of the Ocean Production Enhancement Network, the (Canadian) Federal Panel on Energy, Research and Development, and the U.S. GLOBEC program. This is contribution 35 of the U.S. GLOBEC program, funded jointly by NOAA and NSF.

References

Anderson, C., and Smith, P.C. 1989. Oceanographic observations on the Scotian Shelf during CASP. Atmos.-Ocean, **27**: 130–156.

Beardsley, R.C., and Flagg, C.N. 1976. The water structure, mean currents, and shelf-water/slope-water front of the New England continental shelf. Mem. Soc. R. Sci. Liege, **10**: 209–225.

Bigelow, H.B. 1927. Physical oceanography of the Gulf of Maine. Bull. U.S. Bur. Fish. **40**: 511–1027.

Bretherton, F.P., Davis R.E., and Fandry, C.B. 1976. A technique for objective analysis and design of oceanographic experiments applied to MODE-73. Deep-Sea Res. I **23**: 559–582.

Brown, W.S., and Beardsley, R.C. 1978. Winter circulation in the western Gulf of Maine. Part 1: Cooling and water mass formation. J. Phys. Oceanogr. **8**: 265–277.

Brown, W.S., and Irish, J.D. 1992. The annual evolution of geostrophic flow in the Gulf of Maine: 1986–87. J. Phys. Oceanogr. **22**: 445–473.

Brown, W.S., and Irish, J.D. 1993. The annual variation of water mass structure in the Gulf of Maine: 1986–87. J. Mar. Res. **51**: 53–107.

Bugden, G.L. 1981. Salt and heat budgets for the Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **38**: 1153–1167.

Bugden, G.L. 1991. Changes in the temperature–salinity characteristics of the deeper waters of the Gulf of St. Lawrence over the past several decades. Can. Spec. Publ. Fish. Aquat. Sci. No. **113**: 139–147.

Chapman, D.C., and Beardsley, R.C. 1989. On the origin of shelf water in the Middle Atlantic Bight. J. Phys. Oceanogr. **19**: 384–391.

Chapman, D.C., Barth, J.A., and Beardsley, R.C. 1986. On the continuity of mean flow between the Scotian Shelf and the Middle Atlantic Bight. J. Phys. Oceanogr. **16**: 758–772.

Clarke, R.A., Hill, H.W., Reiniger, R.F., and Warren, B.A. 1980. Current system south and west of the Grand Banks of Newfoundland. J. Phys. Oceanogr. **10**: 25–65.

© 1997 NRC Canada

Csanady, G.T. 1978. The arrested topographic wave. J. Phys. Oceanogr. **8**: 47–62.

Csanady, G.T. 1979. The pressure field along the western margin of the North Atlantic. J. Geophys. Res. **84**: 4905–4915.

Csanady, G.T., and Hamilton, P. 1988. Circulation of slopewater. Continental Shelf Res. **8**: 565–624.

Drinkwater, K., and Taylor, G. 1982. Monthly means of the temperature, salinity and density along the Halifax section. Can. Tech. Rep. Fish. Aquat. Sci. No. 1093.

Drinkwater, K.F., and Trites, R.W. 1986. Monthly means of temperature and salinity in the Grand Banks region. Can. Tech. Rep. Fish. Aquat. Sci. No. 1450.

Drinkwater, K.F., and Trites, R.W. 1987. Monthly means of temperature and salinity in the Scotian Shelf region. Can. Tech. Rep. Fish. Aquat. Sci. No. 1539.

Drinkwater, K.F., Petrie, B., and Sutcliffe, W.H. 1979. Seasonal geostrophic volume transport along the Scotian Shelf. Estuarine Coast. Mar. Sci. **9**: 17–27.

Drinkwater, K.F., Myers, R.A., Pettipas, R.G., and Wright, T.L 1994. Climatic data for the northwest Atlantic: the position of the shelf/slope front and the northern boundary of the Gulf Stream between 50°W and 75°W, 1973–1992. Can. Data Rep. Fish. Ocean Sci. No. 125.

El Sabh, M.I. 1977. Oceanographic features, currents and transport in Cabot Strait. J. Fish. Res. Board Can. **34**: 516–528.

Garrett, C.J.R., Keeley, J.R., and Greenberg, D.A. 1978. Tidal mixing versus thermal stratification in the Bay of Fundy and Gulf of Maine. Atmos.-Ocean, **16**: 403–423.

Gawarkiewicz, G., and Chapman, D.C. 1992. The role of stratification in the formation and maintenance of shelf-break fronts. J. Phys. Oceanogr. **22**: 753–772.

Greatbatch, R.J., and Goulding, A. 1992. A long-time-scale, density-stratified shelf circulation model. Continental Shelf Res. **12**: 115–141.

Greenberg, D.A., and Petrie, B.D. 1988. The mean barotropic circulation on the Newfoundland Shelf and Slope. J. Geophys. Res. **93**: 15541–15550.

Greenberg, D.A., Loder, J.W., Shen, Y., Lynch, D.R., and Naimie, C.E. 1996. Spatial and temporal structure of the barotropic response of the Scotian Shelf and Gulf of Maine to surface wind stress: a model-based study. J. Geophys. Res. (In press)

Hachey, H.B. 1942. The waters of the Scotian Shelf. J. Fish. Res. Board Can. **5**: 377–397.

Han, G., Ikeda, M., and Smith, P.C. 1993. Annual variation of sea-surface slopes over the Scotian Shelf and Grand Banks from Geosat altimetry. Atmos.-Ocean, **31**: 591–615.

Hannah, C.G., Loder, J.W., and Wright, D.G. 1996. Seasonal variation of the baroclinic circulation in the Scotia–Maine region. *In* Buoyancy effects on coastal dynamics. *Edited by* D.G. Aubrey and C.T. Friedrichs. Coastal Estuarine Stud. Vol. 53. American Geophysical Union, Washington, D.C. (In press)

Hopkins, T.S., and Garfield, N. III. 1979. Gulf of Maine intermediate water. J. Mar. Res. **37**: 103–139.

Houghton, R.W., Smith, P.C., and Fournier, R.O. 1978. A simple model for cross-shelf mixing on the Scotian Shelf. J. Fish. Res. Board Can. **35**: 414–421.

Houghton, R.W., Schlitz, R., Beardsley, R.C., Butman, B., and Chamberlain, J.L. 1982. Mid-Atlantic Bight cold pool: the evolution of the temperature structure during summer, 1979. J. Phys. Oceanogr. **12**: 1019–1029.

Koslow, J.A., Thompson, K.R., and Silvert, W. 1987. Recruitment to northwest Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) stocks: influence of stock size and climate. Can. J. Fish. Aquat. Sci. **44**: 26–39.

Lawrence, D.J. 1968. Current meter data from Cabot Strait, 1966. BI Data Series 1968-10-D. Bedford Institute of Oceanography. Dartmouth, N.S.

Loder, J.W., Petrie, B.D., and Gawarkiewicz, G. 1996. The coastal ocean off northeastern North America: a large-scale view. The Sea, **10**. (In press)

Lynch, D.R., and Naimie, C.E. 1993. The M_2 tide and its residual on the outer banks of the Gulf of Maine. J. Phys. Oceanogr. **23**: 2222–2253.

Lynch, D.R., Werner, F.E., Greenberg, D.A., and Loder, J.W. 1992. Diagnostic model for the baroclinic, wind-driven and tidal circulation in shallow seas. Continental Shelf Res. **12**: 37–64.

Lynch, D.R., Ip, J.T.C., Naimie, C.E., and Werner, F.E. 1996. Comprehensive coastal circulation model with application to the Gulf of Maine. Continental Shelf Res. **16**: 875–906.

McLellan, H.J. 1954. Bottom temperature on the Scotian Shelf. J. Fish. Res. Board Can. **11**: 404–418.

Mountain, D.G., and Manning, J.P. 1994. Seasonal and interannual variability in the properties of the surface waters of the Gulf of Maine. Continental Shelf Res. **14**: 1555–1581.

Myers, R.A., Akenhead, S.A., and Drinkwater, K.F. 1990. The influence of Hudson Bay runoff and ice-melt on the salinity of the inner Newfoundland Shelf. Atmos.-Ocean, **28**: 241–256.

Naimie, C.E., and Lynch, D.R. 1993. FUNDY5 users' manual. Numerical Methods Laboratory, Dartmouth College, N.H.

Naimie, C.E., Loder, J.W., and Lynch, D.R. 1994. Seasonal variation of the three-dimensional residual circulation on Georges Bank. J. Geophys. Res. **99**: 15,967–15,989.

Petrie, B. 1990. Monthly means of temperature, salinity and sigma-t for the Gulf of St. Lawrence. Can. Tech. Rep. Hydrogr. Ocean Sci. No. **126**:

Petrie, B.D., and Anderson, C. 1983. Circulation on the Newfoundland continental shelf. Atmos.-Ocean, **21**: 207–226.

Petrie, B.D., and Drinkwater, K. 1993. Temperature and salinity variability on the Scotian Shelf and in the Gulf of Maine 1945–1990. J. Geophys. Res. **98**: 20079–20089.

Petrie, B.D., Topliss, B.J., and Wright, D.G. 1987. Coastal upwelling and eddy development off Nova Scotia. J. Geophys. Res. **29**: 12,979–12,991.

Petrie, B.D., Toulany, B., and Garrett, C. 1988. The transport of water, heat and salt through the Strait of Belle Isle. Atmos.-Ocean, **26**: 234–251.

Ramp, S.R., Brown, W.S., and Beardsley, R.C. 1988. The Nantucket Shoals Flux Experiment. 3. The alongshelf transport of volume, heat, salt and nitrogen. J. Geophys. Res. **93**: 14,039–14054.

Shaw, P.T., and Csanady, G.T. 1983. Self-advection of density perturbations on a sloping continental shelf. J. Phys. Oceanogr. **13**: 769–782.

Sheng, J., and Thompson, K.R. 1996. A robust method for diagnosing regional shelf circulation from scattered density profiles. J. Geophys. Res. **101**: 25647–25659.

Smith, P.C. 1983. The mean and seasonal circulation of southwest Nova Scotia. J. Phys. Oceanogr. **13**: 1034–1054.

Smith, P.C., Petrie, B., and Mann, C.R. 1978. Circulation, variability and dynamics of the Scotian Shelf and Slope. J. Fish. Res. Board Can. **35**: 1067–1083.

Sutcliffe W.H., Loucks, R.H., and Drinkwater, K.F. 1976. Coastal circulation and physical oceanography of the Scotian Shelf and Gulf of Maine. J. Fish. Res. Board Can. **33**: 98–115.

Tee, K.T., Smith, P.C., and LeFaivre, D. 1993. Topographic upwelling off southwest Nova Scotia. J. Phys. Oceanogr. **23**: 1703–1726.

Thompson, K.R. 1986. North Atlantic sea-level and circulation. Geophys. J. R. Astron. Soc. **87**: 15–32.

Thompson, K.R., Loucks, R.H., and Trites, R.W. 1988. Sea surface temperature variability in the shelf-slope region of the northwest Atlantic. Atmos.-Ocean, **26**: 282–299.

Trites, R.W., McLain, D.R., and Ingham, M.C. 1985. Sea surface temperatures along the continental shelf from Cape Hatteras to Hamilton Bank. NAFO Sci. Counc. Stud. **8**: 21–23.

© 1997 NRC Canada

Umoh, J.U., and Thompson, K.R. 1994. Surface heat flux, horizontal advection, and the seasonal evolution of water temperature on the Scotian Shelf. J. Geophys. Res. **99**: 20403–20416.

Wang, D.-P. 1982. Effects of continental slope on the mean shelf circulation. J. Phys. Oceanogr. **12**: 1524–1526.

Weare, B.C. 1977. Empirical orthogonal function analysis of Atlantic Ocean surface temperatures. Q. J. R. Meteorol. Soc. **103**: 467–478.

Weaver, A.J., and Hsieh, W.W. 1987. The influence of buoyancy flux from estuaries on continental shelf circulation. J. Phys. Oceanogr. **17**: 2127–2140.

Wright, D.G., Greenberg, D.A., Loder, J.W., and Smith, P.C. 1986. The steady-state barotropic response of the Gulf of Maine and adjacent regions to surface wind stress. J. Phys. Oceanogr. **16**: 947–966.

Appendix: Correlation scales in density field estimation

The mean hydrographic fields were estimated using the historical temperature–salinity database and 4-D optimal linear interpolation (Bretherton et al. 1976). The interpolation algorithm assumes that the data covariance C depends on the pseudo-distance r between data points (in x,y,z,t space) according to

$$(1)\quad C(r) = e^{-r}(1 + r + r^2/3)$$

where the pseudo-distance is based on the dimensional separation distances in the four independent coordinates, scaled by specified correlation scales. The horizontal correlation scales are specified parametrically, based on the water depth (h) and the local bathymetric gradient vector (∇h) which is taken to have magnitude β and direction ϕ (in degrees) clockwise from north. The basic domain-wide anisotropy in the horizontal scales is specified through along-isobath (-shelf) correlation scales, λ_a, and cross-isobath (-shelf) correlation scales, λ_c, which are computed as follows. For $h \leq 300$ m:

$$(2)\quad \lambda_a = \lambda_o(1 + b_a \sqrt{\beta})$$

$$(3)\quad \lambda_c = \lambda_o(1 - b_c\sqrt{\beta})$$

with the along- (cross-) isobath direction taken as $\phi - 90°$ (ϕ); for 300 m $< h \leq$ 1000 m:

$$(4)\quad \lambda_a = \lambda_o(1 + b_a\sqrt{\beta} \times (h/300))$$

$$(5)\quad \lambda_c = \lambda_o(1 - b_c\sqrt{\beta} + (h - 300)/600)$$

with the along- (cross-) isobath direction taken as $\phi - 90°$ (ϕ); and for $h >$ 1000 m, λ_a = 400 km, λ_c = 60 km, and the along- (cross-) shelf direction taken as 65°T (155°T).

In this parameterization, λ_o is the uniform-depth (isotropic) horizontal correlation scale on the shelf taken as 40 (30) km in winter (summer), and b_a and b_c are scale factors taken as 10 and 3, respectively, in the base case. In the "increased anisotropy" sensitivity case (Table 2), b_a is taken as 15.

In the base cases (and the alternative winter "midtime" case), increased anisotropy is specified for nodes with $h >$ 200 m in the Laurentian Channel, taking λ_a = 150 km, λ_c = 15 km, and 310°T (040°T) for the along- (cross-) channel direction. This increased anisotropy is not included in the sensitivity cases for "Laurentian Channel", "increased anisotropy", and alternative summer "midtime" (Table 2).

© 1997 NRC Canada

Interannual variability (1948–1994) of the CIL core temperature in the Gulf of St. Lawrence

Denis Gilbert and Bernard Pettigrew

Abstract: The interannual variability (1948–1994) of the cold intermediate layer (CIL), defined here as the layer with $T < 3°C$, was investigated for six subregions of the Gulf of St. Lawrence. We first calculated a mean annual cycle of CIL properties for the six subregions (the Estuary, the Northwest, Northeast, Central, and Southern Gulf, and Cabot Strait). The midsummer warming rates thus obtained were then used to construct time series of the CIL core temperature extrapolated to July 15, using all available data from May 1 to September 30 of each year. Our most important result is that the mid-summer CIL core temperature was below normal from 1986 to 1994, this cold period being most intense from 1990 to 1994. We correlated the time series of CIL core temperature with average winter air temperatures from several weather stations inside and outside the Gulf to try to distinguish between local and remote atmospheric forcing and obtained the highest correlations with weather stations from the west coast of Newfoundland.

Résumé : Nous avons étudié la variabilité interannuelle (1948–1994) de la couche intermédiaire froide (CIF), définie ici comme étant la couche où la température de l'eau est inférieure à 3°C, dans le golfe du Saint-Laurent. Nous avons d'abord calculé un cycle annuel moyen des propriétés de la CIF pour six sous-régions du golfe (l'estuaire, le nord-ouest, le nord-est, le centre, le sud et le détroit de Cabot). Les taux de réchauffement estivaux ainsi obtenus furent utilisés pour créer une série chronologique de la température du coeur de la CIF, extrapolée au 15 juillet, en nous servant de toutes les données disponibles entre le 1er mai et le 30 septembre de chaque année. Nous avons trouvé que de 1986 à 1994, la température estivale du coeur de la CIF était sous la normale, et que cette période froide fut particulièrement intense de 1990 à 1994. Nous avons également corrélé les séries chronologiques de température du coeur de la CIF avec les températures atmosphériques hivernales moyennes de plusieurs stations météorologiques à l'intérieur et à l'extérieur du golfe afin de distinguer entre le forçage atmosphérique local et éloigné. Les plus fortes corrélations furent obtenues avec les stations météorologiques de la côte ouest de Terre-Neuve.

Introduction

The cold intermediate layer (CIL) is one of the most striking features of the temperature and salinity structure of the Gulf of St. Lawrence from spring to fall. In their review of the physical oceanography of the Gulf, Koutitonsky and Bugden (1991) pointed out that in winter, the water column can be roughly described as a two-layer system, with a cold and relatively fresh surface layer overlying a warmer and saltier bottom layer. At the onset of spring, the ice melts and the top of the surface layer begins to warm, while the deeper portion of what used to be the winter surface mixed layer remains at near-freezing temperatures. As spring progresses into summer, the top layer warms much more rapidly than the waters underneath, and the water column becomes a three-layer system, with a warm and relatively fresh surface layer, a CIL, and a warmer and saltier bottom layer. The temperature contrast between the surface layer and the CIL is most pronounced in mid-August, when water temperatures close to 0°C can often be found only 60 m below the surface which may be at a temperature as high as 18°C.

Received March 8, 1995. Accepted March 13, 1996.
J13438

D. Gilbert and B. Pettigrew. Ministère des Pêches et des Océans, Institut Maurice-Lamontagne, MPO-Québec, Division de la Productivité des Océans, C.P. 1000, Mont-Joli, QC G5H 3Z4, Canada.

Several studies have shown that the volume of the Gulf's CIL is maximum by the end of March, and then decreases at a relatively steady rate from spring to fall. Lauzier and Bailey (1957), defining the CIL as waters with $T < 0°C$ and an average salinity (S) of 32.4, found that the CIL occupied 26% of the volume of the Gulf in the spring, 12% in summer, and only 4% in early and late fall. The reduction of the volume of waters with $T < 0°C$ by late autumn was confirmed by Petrie et al. (1988*b*), who analyzed 12 years (1969–1980) of hydrographic data from the mid-November ice forecast cruise. Out of a total of 243 stations deeper than 50 m, they only found 28 stations with $T < 0°C$ waters. By the end of December or early January, atmospheric cooling and intense vertical mixing associated with the passage of storms cause the surface layer to cool and eventually merge with the CIL, so that the water column can again be roughly described as a two-layer system, with a cold and fresh surface layer overlying a warmer and saltier bottom layer.

Using bathythermograph data from 1952 to 1962 and a different definition for the CIL, $T < 1.5°C$, Banks (1966) quantified the spring to fall warming and thinning rates of the CIL. In three representative sections of the deep channels of the Gulf, he estimated that the core temperature of the CIL warms at a rate of about 0.2°C/mo from April to November, while its thickness decreases by 5–10 m/mo. By studying the horizontal distribution of the CIL core temperature for three periods corresponding to spring, summer, and fall, he concluded that inflow of water through Cabot Strait cannot be the source of the Gulf's CIL, as the CIL core temperatures were

© 1997 NRC Canada

always warmer in Cabot Strait than in the rest of the Gulf. To investigate the role of in situ cooling as a likely mechanism for the production of the CIL, he performed a linear regression analysis of mean winter air temperature at the Magdalen Islands against the Gulf's CIL core temperature extrapolated to July 15 of the following summer and obtained a high correlation coefficient ($r = 0.87$). Repetition of the same analysis with a weather station in southern Labrador gave a lower correlation coefficient ($r = 0.68$), which led Banks (1966) to suggest that the Gulf's CIL was most probably formed in situ. In support of this conclusion, he estimated that the flow through the Strait of Belle Isle could only account for about 14% of the volume of waters with $T < 1.5$°C found in the Gulf of St. Lawrence at the end of March.

However, Petrie et al. (1988*b*) pointed out that Banks' estimate is equivalent to 26% of the volume of waters with $T < 0$°C at the end of March, taking into account the volumetric ratio of waters with $T < 0$°C to those with $T < 1.5$°C (Forrester 1964). They also calculated their own estimates of flow through the Strait of Belle Isle, based on current-meter data from the 1980 summer and on geostrophic leveling of the "permanent" tide gauges that were maintained on both sides of the Strait in the 1970s. Petrie et al. (1988*b*) estimated that from January to May, the 1969–1978 average inflow through the strait of Belle Isle was 0.3×10^6 m^3/s. The average inflow from January to March was somewhat higher (0.4×10^6 m^3/s) and could account for 35% of Forrester's (1964) estimate of the volume of waters with $T < 0$°C and $S > 32$ at the end of March (9.2×10^{12} m^3). However, if we take into account uncertainties due to the possible contribution of December flow with the appropriate T and S properties, as well as uncertainties related to changes in gnomon elevation at the tide gauge sites, as discussed in Petrie et al. (1988*b*), the flow through the Strait of Belle Isle could actually account for between 26 and 53% of the volume of the Gulf's CIL at the end of March. Using a multiple regression technique, Petrie et al. (1988*b*) concluded that for the period of nine years from 1970 to 1978, the average December–May air temperature at the Magdalen Islands and the average January to May inflow through the Strait of Belle Isle together accounted for 48% of the variability ($r = 0.69$) of the CIL's temperature, as represented by the average temperature of the 50–80 m layer in the Gulf.

The studies of Banks (1966), Bugden et al. (1982, p. 81), and Petrie et al. (1988*b*) have all shown that the properties of the Gulf's CIL are subject to large interannual variations. It is believed that such interannual changes in the core temperature and thickness of the CIL could have an impact on the development of Atlantic cod (*Gadus morhua*) eggs released in the water column by the spawning northern Gulf cod stock in the spring, and thus affect its recruitment (P. Ouellet, Institut Maurice-Lamontagne, Mont-Joli, Qué., personal communication). Changes in CIL properties, especially temperature, could also affect the growth rate and perhaps even the feeding rate of juvenile cod, which are often found within the CIL during the summer in the Northern Gulf (J. Gagné, Institut Maurice-Lamontagne, Mont-Joli, Qué., personal communication). The CIL therefore seems to be an important part of the environment affecting the early life stages of cod in the Gulf. Moreover, although adult cod do not occupy CIL waters in the Gulf during the winter, they live closer to the depth range of the CIL during the summer, so that their physiological condition could in principle be affected by the temperature of the CIL (Y. Lambert, Institut Maurice-Lamontagne, Mont-Joli, Qué., personal communication). In this paper, our aim is to document the interannual changes that have occurred in the core temperature of the Gulf's CIL from 1948 to 1994, given the database of temperature available to us.

Methods

Temperature and salinity database

As part of the Atlantic Fisheries Adjustment Program (AFAP), a database of temperature and salinity was recently created at the Bedford Institute of Oceanography (BIO) from the data archive of the Marine Environment Data Service (MEDS). The AFAP database is essentially an edited version of the MEDS archive. Profiles for which problems were flagged by the MEDS quality checks were either excluded from the AFAP database or were included after some appropriate corrections (K. Drinkwater, Bedford Institute of Oceanography, Dartmouth, N.S., personal communication). As of May 1994, the AFAP database for the Gulf of St. Lawrence region consisted of 44 973 profiles, largely dominated by mechanical bathythermograph and bottle data, with 23 487 and 14 958 profiles, respectively, compared with only 3752 CTD-down profiles. There were also 1623 expendable bathythermograph (XBT) profiles, 502 digital bathythermograph (DBT) profiles, 246 bathy-message profiles, 212 CTD-up profiles, and 193 TESAC-message (CTD) profiles. Since bottle measurements are taken at discrete depths and generally have a poor vertical resolution, we did not include them in our study of the CIL and focused instead on data from continuous profilers such as bathythermographs and CTDs. Note that the AFAP database is currently being updated as new temperature and salinity data become available to MEDS. The number of CTD profiles from the Gulf of St. Lawrence in the MEDS and AFAP databases should therefore greatly increase in the next few years. In addition to the AFAP database, we used temperature and salinity data collected during the 1987–1994 late summer groundfish surveys in the Northern Gulf (1165 CTD and 67 XBT profiles) and from the 1993 and 1994 September groundfish surveys in the Southern Gulf (378 CTD profiles).

Choice of subregions

We subdivided the Gulf into six subregions for our study of the CIL (Fig. 1). Our choice was partly based on the number of temperature profiles available in each region and on a priori knowledge about the physical oceanography of the Gulf (Koutitonsky and Bugden 1991). They are similar to the six subregions used by Déry (1992) in his study of the interannual variability of the ice cover in the Gulf of St. Lawrence. Subregion I, the Estuary, has the lowest surface salinities due to freshwater input from the St. Lawrence River and is a region where intense vertical mixing and upwelling take place near the head of the Laurentian Channel (Koutitonsky and Bugden 1991, p. 75). Subregion II, the Northwest Gulf, can be seen as a transition zone between the Estuary and the Central Gulf. Subregion III, the Northeast Gulf, is the region of the Gulf most directly affected by inflow of cold water from the Labrador shelf through the Strait of Belle Isle. Subregion IV, the Central Gulf, is some distance away from the direct influence of the Estuary and the two open boundaries of the Gulf (Cabot Strait and the Strait of Belle Isle). Subregion V, the Cabot Strait, is directly affected by the exchange of waters between the Gulf of St. Lawrence and the Atlantic Ocean. And finally, subregion VI, the Southern Gulf, is a shallow region of the Gulf where much of the bottom area is in direct contact with the CIL; vertical profiles of temperature do not entirely cross the CIL in this region, thus precluding estimates of its thickness amongst other properties.

CIL definition

As implied by the word "intermediate", the CIL is a layer of cold

© 1997 NRC Canada

Fig. 1. Map of the Gulf of St. Lawrence showing the location of the six subregions used in this study: subregion I, the Estuary; subregion II, the Northwest Gulf; subregion III, the Northeast Gulf; subregion IV: the Central Gulf; subregion V, Cabot Strait; subregion VI, the Southern Gulf. The locations of weather stations mentioned in the text are also indicated.

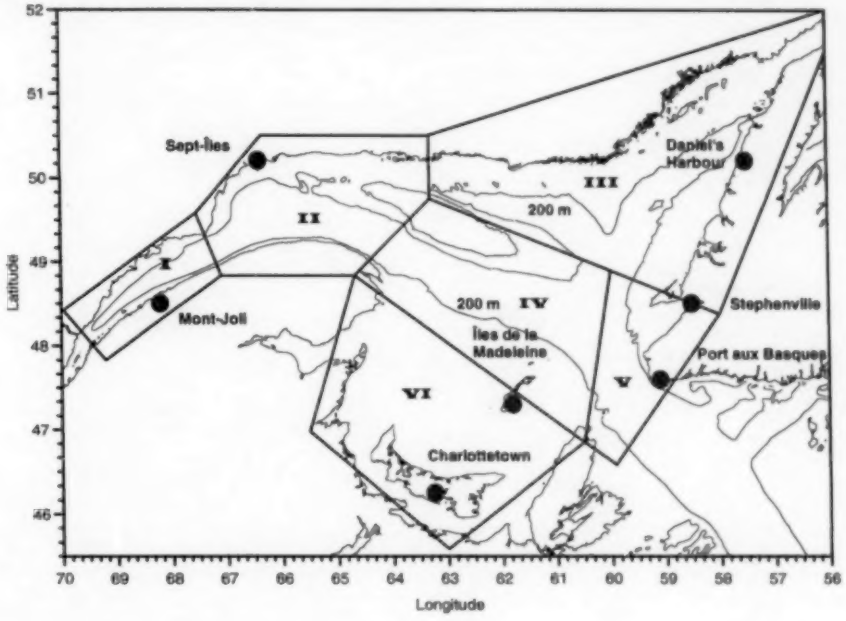
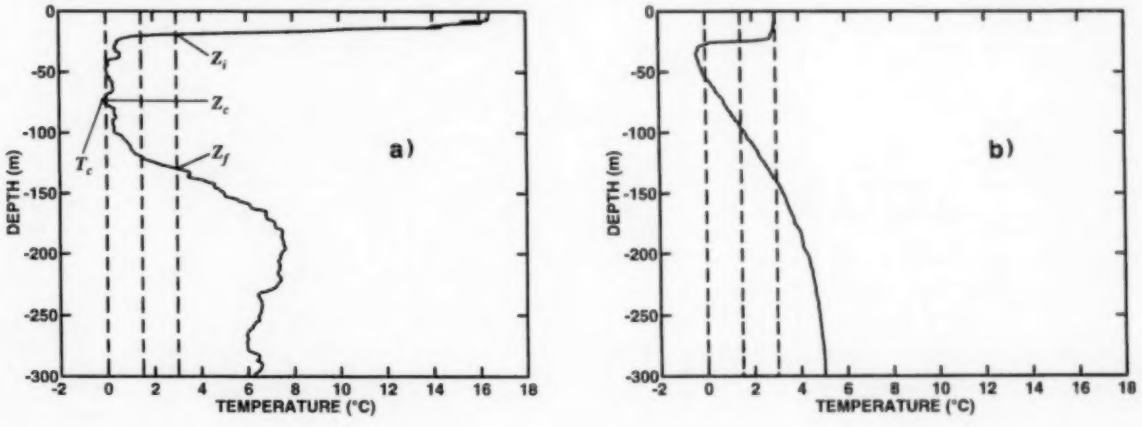


Fig. 2. (*a*) Vertical profile of temperature taken on the eastern side of Cabot Strait on August 18, 1993. The vertical lines at $T = 0$°C, $T = 1.5$°C, and $T = 3$°C show some of the possible definitions for the CIL. The depth (Z_c) and the temperature (T_c) of the core of the CIL are indicated. The depths at which the CIL begins and ends (Z_i and Z_f) are also shown for the $T < 3$°C CIL definition. (*b*) Vertical profile of temperature taken in the Northwest Gulf of St. Lawrence on October 25, 1993, when the surface temperature dropped to 3°C.



water sandwiched between warmer layers of water both above and below. A vertical profile of temperature taken in eastern Cabot Strait in August 1993 shows some of the temperature limits (0, 1.5, and 3°C) that could be used to define the Gulf's CIL (Fig. 2*a*). Lauzier and Bailey (1957) defined the CIL as waters with $T < 0$°C whereas Banks (1966) and Bugden et al. (1982) defined it as the layer with waters with $T < 1.5$°C. To determine what definition would best characterize the full range of interannual variability of the Gulf's CIL core temperature over the 1948–1994 period, we used a subroutine that found the temperature minima of profiles that reached a depth of at least 100 m in the five deep subregions of the Gulf and reached a depth of at least 60 m in the Southern Gulf. Upon examining the results, we decided to use $T < 3$°C as our definition of the CIL, the number of rejected profiles from warmer years in the temperature database then being negligible. To understand the consequences of this choice, note that the values of Z_c and T_c would be the same whether we use $T < 1.5$°C or $T < 3$°C as our definition of the CIL, but the values of Z_i and Z_f would be different (Fig. 2*a*). In other words, Z_c and T_c are the same for both CIL definitions provided that $T_c < 1.5$°C, but the CIL thickness is different, the $T < 3$°C CIL

© 1997 NRC Canada

Table 1. Mean monthly rates of change of CIL properties for the May–September period.

	Estuary	Northwest Gulf	Northeast Gulf	Central Gulf	Cabot Strait
Z_i (m/mo)	6.5	6.4	8.5	5.3	6.7
Z_f (m/mo)	–3.1	–0.7	0.0	–0.7	–0.9
Thickness (m/mo)	–9.6	–7.1	–8.5	–6.0	–7.6
Z_c (m/mo)	0.6	2.5	1.0	–0.4	5.5
T_c (°C/mo)	0.30	0.19	0.15	0.08	0.11
Heat gain (W/m^2)	72	36	41	21	34

Note: Z_i is the depth of the upper 3°C isotherm, Z_f is the depth of the lower 3°C isotherm, and CIL thickness is given by $Z_f - Z_i$. CIL core temperature T_c, depth Z_c, and heat content are defined in the text. Rate of change of CIL heat content is expressed in the customary units of W/m^2. In the Southern Gulf, the rate of change of the temperature minimum T_m is 0.13°C/mo, and its depth Z_m increases at a rate of 3.0 m/mo.

always being thicker than the $T < 1.5$°C CIL (Fig. 2*a*). Another difference between the two definitions is that the $T < 3$°C CIL has a slightly shorter life span than the T < 1.5°C CIL for any given year, as the surface temperature rises to 3°C later in the spring and drops to 3°C earlier in the fall. For instance, a temperature profile taken in the Northwest Gulf on October 25, 1993 (Fig. 2*b*), shows that the surface temperature had just dropped to 3°C, so that the $T < 3$°C CIL locally ceased to exist as a separate layer at that time. The $T < 1.5$°C and $T < 0$°C definitions of the CIL could still be used on that specific date (Fig. 2b), but they would in turn cease to be useful CIL definitions only a few weeks later, as the surface temperature drops below 1.5°C, and then below 0°C.

Computation of CIL statistics

For the five deep subregions of the Gulf, we calculated the mean and standard deviation of various CIL properties in the following manner. First, we searched the historical database of temperature and salinity to select profiles that reached a depth of at least 100 m and were between specific dates (e.g., August 1–30, 1971). A further selection was then made according to whether or not the profiles reached the lower 3°C isotherm of the CIL, typically found between about 140 and 180 m depth; we only kept the profiles that entirely crossed the CIL. The values of the upper, core, and lower depths of the CIL (Z_i, Z_c, and Z_f, respectively) and the CIL core temperature T_c (Fig. 2*a*) were determined for each profile, together with the CIL thickness. Moreover, we calculated the CIL heat content for each profile, defined here as

$$\int_{Z_i}^{Z_f} \rho\, c_p (T - 3°C) dz$$

where the density of seawater ρ is assumed constant (1025 kg/m^3), the specific heat of seawater, c_p, is also assumed constant (4000 J·kg^{-1}·°C^{-1}), and the water temperature T is a function of depth. The CIL heat content as defined here is therefore proportional to the area of the temperature profile to the left of the 3°C line in Fig. 2. Finally, the means and standard deviations of Z_i, Z_c, Z_f, T_c, CIL thickness, and heat content were computed from all the selected profiles.

For the Southern Gulf, a different method had to be used because the profiles generally did not entirely cross the CIL as defined here ($T < 3$°C). First, we searched the historical database of temperature and salinity to select profiles that reached a depth of at least 60 m and were within specific dates (e.g., May 1 – September 30, 1962). For each of these profiles, we determined the value of the temperature minimum T_m, together with the depth Z_m at which the minimum occurred, and then computed the mean and standard deviation of these properties from all the selected profiles.

Calculation of the July 15 CIL core temperature

Our original intent was to document the interannual variability of the CIL for the period of the year corresponding to the late summer groundfish survey in the Gulf of St. Lawrence: August 31 – October 6 in the Southern Gulf (Chouinard and Swain 1994) and August 11 – September 16 in the Northern Gulf (Gratton et al. 1994). However, we faced serious problems of data scarcity everywhere but in the Southern Gulf (Fig. 1), for which there were 44 years of data from a possible total of 47 for the 1948–1994 period. By contrast, there were only 16 years with data from the Estuary, 24 years with data from the Northwest Gulf, 17 years with data from the Northeast Gulf, 33 years with data from the Central Gulf, and 27 years with data from Cabot Strait.

By widening our search in the AFAP database to the May 1 – September 30 period for all six regions, a time of the year during which the CIL is usually well defined, we significantly reduced the number of gaps in the 1948–1994 time series. There were now 26 years with data from the Estuary, 39 years with data from the Northwest Gulf, 38 years with data from the Northeast Gulf, 46 years with data from the Central Gulf, 41 years with data from Cabot Strait, and 47 years (no gaps) with data from the Southern Gulf. To take into account the year-to-year differences that occurred in the mean date of measurements, the CIL core temperatures were extrapolated to a common midsummer date, July 15, using the regional climatological May–September warming rates of T_c (Table 1). A *composite index* of equally weighted CIL core temperature anomalies for the Northwest Gulf, Northeast Gulf, Central Gulf, and Cabot Strait was then calculated, the Estuary being left out of the index because of the less abundant data from this region. A separate time series of temperature minima extrapolated to July 15 was calculated for the Southern Gulf.

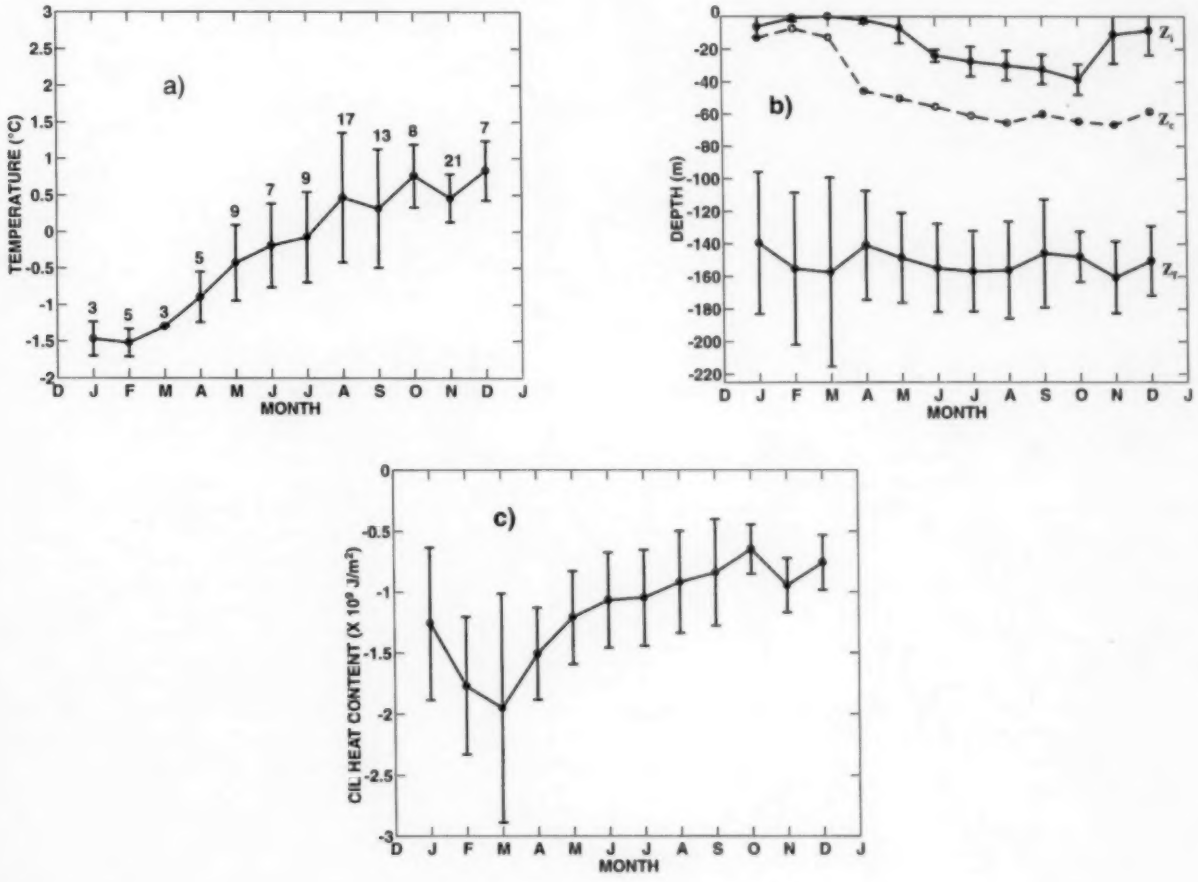
Results

CIL annual cycle

A climatological mean annual cycle of the CIL was computed for each subregion, giving equal weight to each year in computing the monthly means and standard deviations of each CIL property. For the Northwest Gulf, we show the annual cycle of the CIL core temperature (Fig. 3*a*), the annual cycle of the CIL core depth Z_c and the depths Z_i and Z_f at which the CIL begins and ends (Fig. 3*b*), and the annual cycle of the CIL heat con-

© 1997 NRC Canada

Fig. 3. Mean annual cycle of the CIL, defined as waters with $T < 3.0°C$, in the Northwest Gulf. (*a*) temperature T_c of the core of the CIL; (*b*) depths of the upper and lower 3.0°C isotherms (Z_i and Z_f) together with the depth Z_c of the CIL core; (*c*) CIL heat content. The error bars are 1 standard deviation long, indicating interannual variability. The number of years from which the monthly means and standard deviations were calculated is shown above each error bar in Fig. 3*a*.



tent (Fig. 3*c*). Standard deviations (Fig. 3) give us a measure of the interannual variability. The CIL core temperature (T_c) is close to freezing temperatures from January to March and then increases at a more or less steady rate from April to December (Fig. 3*a*). The CIL core temperature changes abruptly from December (1°C) to January (−1.5°C) because the minimum temperature of the water column quickly drops to freezing temperatures when ice starts to form at the surface. Hence the depth of the temperature minimum or CIL core, Z_c, rises abruptly from December to January (Fig. 3*b*); it is less than 20 m deep from January to March, quickly drops to about 45 m in April, and then deepens more slowly to reach 65 m depth by August, after which it remains relatively constant until December. As could be expected, the annual cycle of CIL thickness is entirely due to changes in the depth Z_i of the upper 3°C isotherm (Fig. 3*b*). The depth Z_f of the lower 3°C isotherm remains essentially constant throughout the year at about 150 m (±30 m), but is subject to greater interannual variability than Z_i as indicated by the larger standard deviations (Fig. 3*b*). Finally, the CIL heat content quickly decreases during the period of CIL formation, from December to March (Fig. 3*c*). The largest monthly decrease in CIL heat content, equivalent to a heat loss of about 228 W/m^2, takes place from January to February when the CIL has merged with the surface layer and is in direct contact with the atmosphere and/or ice cover. The CIL heat content quickly increases from March to May and then increases at a much slower rate until October due to the relative isolation from the surface provided by a strong summer pycnocline near the surface.

The CIL annual cycle in the other regions of the Gulf follows the same overall pattern as in the Northwest Gulf, although there are regional differences in the monthly averaged values and rates of change of most CIL properties. The annual cycles of T_c in the Estuary and Northwest Gulf are similar, except for the January–April period when the CIL core temperatures appear to be systematically lower in the Northwest Gulf than in the Estuary by about 0.3–0.4°C (Fig. 4). In the Southern Gulf, the most distinctive feature is the warmer minimum temperature from October to January than in the other two regions, the difference being as large as 1°C

© 1997 NRC Canada

Fig. 4. Mean annual cycle of the CIL core temperature in the Estuary (long-dashed line), the Northwest Gulf (continuous line), and the Southern Gulf (short-dashed line).

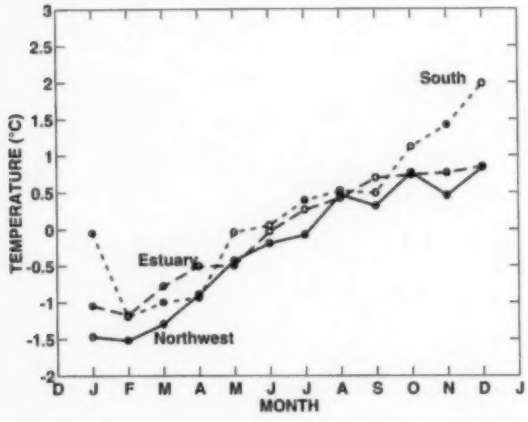
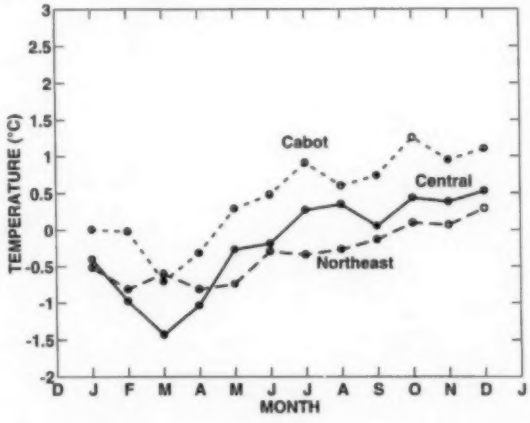


Fig. 5. Mean annual cycle of the CIL core temperature in the Northeast Gulf (long-dashed line), the Central Gulf (continuous line), and Cabot Strait (short-dashed line).



in December (Fig. 4). This is probably because the surface waters of the Southern Gulf become much warmer than in the other two regions during the summer (Petrie 1990), so that more heat can be transferred downwards during the fall when the surface layer deepens. From May to December in the other subregions (Fig. 5), the CIL core temperature is always coldest in the Northeast Gulf, warmest in Cabot Strait, and somewhere between these two extremes in the Central Gulf, in agreement with the earlier findings of Banks (1966). The CIL core temperature in Cabot Strait is about 0.5°C warmer than in the Central Gulf throughout the year (Fig. 5). From January to April, the CIL core temperatures in the Central Gulf and Northeast Gulf are similar, except for a suspiciously warm March in the Northeast Gulf that is based on a single temperature profile from a single year (1956).

Mean midsummer CIL properties in each subregion

The May–September period corresponds to a part of the annual cycle when the CIL is usually well established and evolves at a relatively slow and steady rate (Figs. 3, 4, and 5). It also corresponds to the part of the year for which we have the largest amount of historical temperature and salinity data (Petrie 1990). We therefore decided to use this period to compare the CIL properties of each region and their rate of change. Climatological midsummer CIL properties for the five deep subregions were calculated from the average of the May–September monthly means (Table 2). We find that the CIL is coldest, thickest, and has the lowest heat content in the Northeast Gulf, while at the other extreme the CIL is warmest and has the largest heat content in Cabot Strait. The upper 3°C isotherm is about 25 m deep everywhere, the lower 3°C isotherm is between 150 and 170 m deep, and the core of the CIL is between 55 and 75 m deep, closer to the upper 3°C isotherm than to the lower 3°C isotherm. The CIL properties from the Southern Gulf were not included in Table 2 because of a difference in methods. However, for the May–September period in the Southern Gulf, the average value of the temperature minimum T_m is 0.36°C, and it occurs at a depth Z_m of 61.2 m.

We also calculated the monthly rates of change of CIL properties from the difference between the May and September climatological monthly means (Table 1). The CIL thickness decreases at rates that range between 6 and 10 m/mo, in agreement with Banks' (1966) estimate of 5–10 m/mo despite the difference in CIL definitions. As could be expected, we also found that the thinning of the CIL is almost entirely due to changes in the depth of the upper 3.0°C isotherm Z_i. The depth of the lower 3°C isotherm Z_f remains essentially constant in all regions, except perhaps for the Estuary where it shoals at the rate of about 3 m/mo. The May–September warming rates of the CIL core temperature range from 0.08 to 0.30°C/mo. Interestingly, we find that the largest values of CIL thinning rate, warming rate, and heat gain occur in the Estuary whereas the lowest values occur in the Central Gulf. This suggests that during the summer, vertical mixing and upwelling are probably most intense in the Estuary and least intense in the Central Gulf. In the Southern Gulf, the rate of change of the temperature minimum T_m is 0.13°C/mo, and its depth Z_m increases at the rate of 3.0 m/mo.

Interannual variability of the July 15 CIL core temperature

The composite index of midsummer CIL core temperature for subregions II–V (Fig. 1) of the Gulf of St. Lawrence exhibits variability on time scales that range from interannual to interdecadal (Fig. 6). From 1948 to 1994, there were three generally warm periods, 1949–1955, 1965–1971, and 1980–1983, and three generally cold periods, 1961–1964, 1972–1977, and 1986–1994. The most recent of these cold periods has been the most intense of all, as seven of the eight coldest years in the entire record (47 years) occurred between 1986 and 1994. Similarly, cold temperatures were also observed since 1986 at 75 m depth over St. Pierre Bank on the southern Newfoundland shelf (Colbourne 1994). The warmest CIL core temperature in the Gulf occurred in 1970, consistent with the work of Petrie et al. (1988*b*), who used the average temperature of the 50–80 m layer in the Gulf as an indicator of the CIL temperature from 1970 to 1978 and found that the warmest CIL for that 9-yr period also occurred in 1970.

The temperature minima in the Southern Gulf also exhibit

© 1997 NRC Canada

Table 2. Average midsummer properties of the CIL, calculated from the May–September monthly means.

	Estuary	Northwest Gulf	Northeast Gulf	Central Gulf	Cabot Strait
Z_1 (m)	23.2	24.1	24.1	26.4	28.2
Z_f (m)	156.7	152.4	168.9	159.7	157.2
Thickness (m)	133.5	128.3	144.8	133.3	129.0
Z_c (m)	66.2	58.5	73.1	67.6	74.6
T_c (°C)	0.17	0.02	−0.36	0.04	0.60
Heat content (10^9 J/m^2)	−0.98	−1.02	−1.36	−1.07	−0.89

Note: Symbols as defined in Table 1. In the Southern Gulf, the May–September average value of the temperature minimum T_m is 0.36°C and occurs at a depth Z_m of 61.2 m.

Fig. 6. Deviations from the 1948–1994 mean CIL core temperature in the Gulf of St. Lawrence extrapolated to July 15 (0.08°C), using all available data between May 1 and September 30 of each year in the Northwest Gulf, Northeast Gulf, Central Gulf, and Cabot Strait.

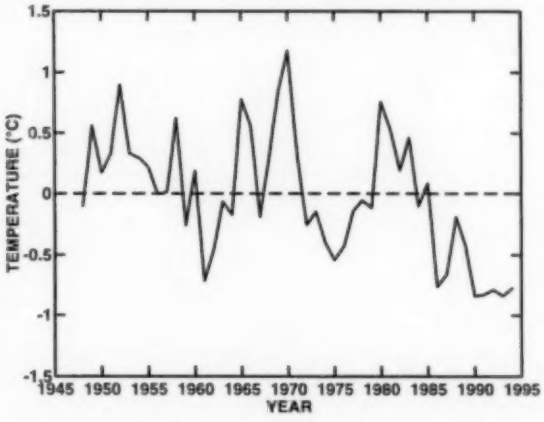
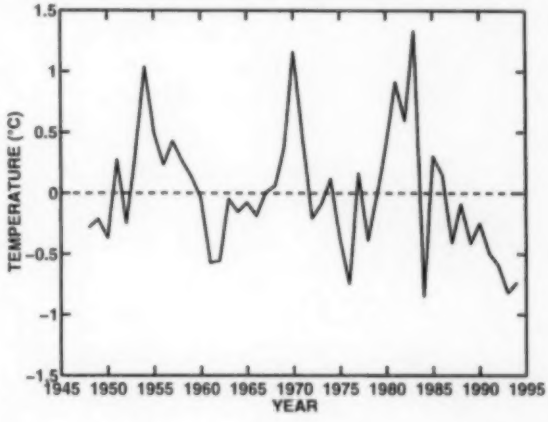


Fig. 7. Deviations from the 1948–1994 mean temperature minimum in the Southern Gulf extrapolated to July 15 (0.36°C), using all available data between May 1 and September 30 of each year.



a great deal of interannual and interdecadal variability (Fig. 7). Warm periods occurred in 1953–1959, 1969–1971, and 1980–1983, while cold periods occurred in 1948–1950, 1961–1962, 1975–1976, and 1987–1994, plus a very cold isolated year in 1984. The latter anomaly (1984) corresponds to a strong positive anomaly in Swain's (1993) time series of the Southern Gulf area with bottom temperatures less than 1°C and less than 0°C. It also coincides with the very cold CIL observed in 1984 on the Newfoundland shelf (Petrie et al. 1988*a*; Colbourne and Senciall 1993).

Regression analysis between July 15 CIL core temperature and winter air temperature

Banks (1966) has shown that the mean winter air temperature over the Gulf is certainly one of the key factors affecting the Gulf's CIL core temperature the following summer. We use his index of the average December–March air temperature as a measure of the severity of the winter at weather stations around the Gulf: Mont-Joli, Sept-Îles, and Îles de la Madeleine (Québec), Charlottetown (Prince Edward Island), Port aux Basques, Stephenville, and Daniel's Harbour (Newfoundland). To examine the role of remote atmospheric forcing upstream of the Strait of Belle Isle, we also included air temperatures from Cartwright, Southern Labrador, in our analyses. The correlation coefficients obtained with a simple linear regression analysis were all positive (Table 3), meaning that years with warmer than usual winter air temperatures over the Gulf generally correspond to warmer than usual CILs the following summer. We find that the correlations with winter air temperature are always higher for the Gulf composite index (subregions II–V, Fig.1) than for the Southern Gulf index (subregion VI). We believe that this is partly due to the greater amount of averaging that went into producing the Gulf composite index, but also due to the fact that in the Southern Gulf, our method of calculating the water column's temperature minimum is not as reliable when this minimum occurs deeper than 60 m.

The three highest correlations between the Gulf composite index of CIL core temperature and winter air temperature were obtained with weather stations from the west coast of Newfoundland: Port aux Basques ($r = 0.74$), Stephenville ($r = 0.73$), and Daniel's Harbour ($r = 0.78$). Interestingly, the correlation between the CIL core temperature in the Gulf and the North Atlantic Oscillation (NAO) index is much weaker ($r = -0.28$), despite the fact that strong positive anomalies of the NAO index are generally associated with cold air tempera-

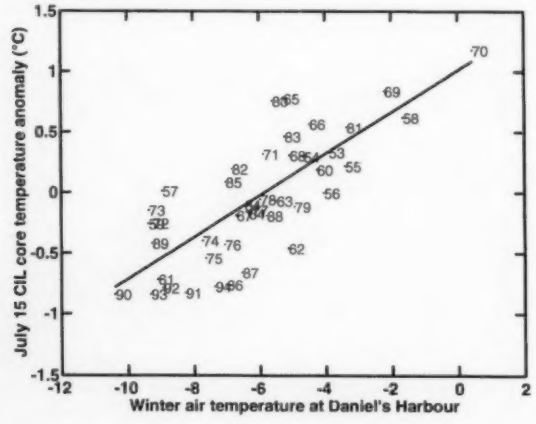
© 1997 NRC Canada

Table 3. Results of the linear regression analysis between the CIL core temperature extrapolated to July 15 and the December–March average winter air temperature at a few weather stations around the Gulf of St. Lawrence.

		Southern Gulf			Composite index (deep regions)		
Weather station	Period	r	r^2	p	r	r^2	p
Mont-Joli	1948–1990 (43)	0.35	0.12	0.021	0.56	0.31	<0.01
Sept-Îles	1948–1994 (47)	0.43	0.18	<0.01	0.62	0.38	<0.01
Îles de la Madeleine	1984–1994 (44) (missing 1983, 1984, and 1986)	0.50	0.25	<0.01	0.68	0.46	<0.01
Charlottetown	1948–1990 (43)	0.41	0.17	<0.01	0.58	0.34	<0.01
Port aux Basques	1956–1992 (37)	0.41	0.17	0.011	0.74	0.55	<0.01
Stephenville	1948–1994 (46) (missing 1951)	0.51	0.26	<0.01	0.73	0.53	<0.01
Daniel's Harbour	1953–1994 (42)	0.55	0.30	<0.01	0.78	0.61	<0.01
Cartwright	1948–1994 (47)	0.46	0.21	<0.01	0.65	0.43	<0.01

Note: The periods for which the regressions were computed are indicated, with the number of years assumed equal to the number of degrees of freedom written in parentheses ($p < 0.05$ in all cases, but a more careful analysis should take into account the autocorrelation in the time series which would reduce the number of degrees of freedom).

Fig. 8. Scatter diagram of the average winter air temperature at Daniel's Harbour against the composite index of the Gulf's CIL core temperature extrapolated to July 15 of the following summer from 1953 to 1994 ($r = 0.78$, $r^2 = 0.61$). The numbers on the plot refer to the last two digits of the years of observations. The linear regression line is T (CIL) = 0.173·T (air) + 1.01.



tures, heavy ice, and intense CILs on the Labrador and Newfoundland shelves (Colbourne et al. 1994). This suggests that local processes taking place at a smaller scale within the Gulf of St. Lawrence actually play a major role in the formation of the CIL. A scatter diagram of the Gulf composite index of CIL core temperature against mean December–March winter air temperature at Daniel's Harbour shows that years with warm winter air temperature at Daniel's Harbour generally correspond to warm CILs the following summer and, conversely, that years with cold winter air temperature generally correspond to cold CILs the following summer (Fig. 8). However, there still remains a great deal of scatter in the data, as the regression only accounts for 61% of the total variance.

The 1953–1994 mean winter air temperature at Daniel's Harbour is shown in Fig. 9 together with similar data from 1945 to 1994 for Sept-Îles. The most striking difference between the two time series is that the 1961–1990 mean winter air temperature is 5°C warmer at Daniel's Harbour (−6.28°C) than at Sept-Îles (−11.35°C), even though the two weather stations are located essentially at the same latitude (Fig. 1). At Daniel's Harbour, the six consecutive winters from 1989 to 1994 have all been characterized by below-normal air temperatures (Fig. 10). The five consecutive winters from 1972 to 1976 were also below normal. There were warm periods from 1953 to 1956 and from 1968 to 1970. The period from 1977 to 1988 was characterized by near-normal winter air temperatures, except for a relatively warm year in 1981. At Sept-Îles, we find the same overall pattern, but the anomalies sometimes differ significantly from those at Daniel's Harbour (Fig. 10). For example, the 1960, 1966, and 1987 positive anomalies were about 1°C larger at Sept-Îles than at Daniel's Harbour whereas the 1970 positive anomaly was about 6°C larger at Daniel's Harbour than at Sept-Îles.

According to Drinkwater and Pettipas (1993), the winds over the Gulf are generally from the northwest during the winter. The air masses affecting Sept-Îles in winter would then be continental whereas the air masses affecting Daniel's Harbour would have a more marine character, provided of course that the Northeast Gulf is not completely ice covered. Local heat exchange between the ocean and the atmosphere could then be responsible for the generally higher winter air temperatures observed at Daniel's Harbour (Fig. 9). The 1962–1987 median ice extent limits drawn by Côté (1989) for the whole eastern Canadian seaboard show that the western Newfoundland coast generally remains ice free as far as Daniel's Harbour until mid-February (Fig. 11), thus allowing

© 1997 NRC Canada

Fig. 9. December–March average air temperature at Sept-Îles, Québec (broken line), and at Daniel's Harbour, on the west coast of Newfoundland (continuous line). The 1961–1990 mean is −6.28°C at Daniel's Harbour and −11.35°C at Sept-Îles.

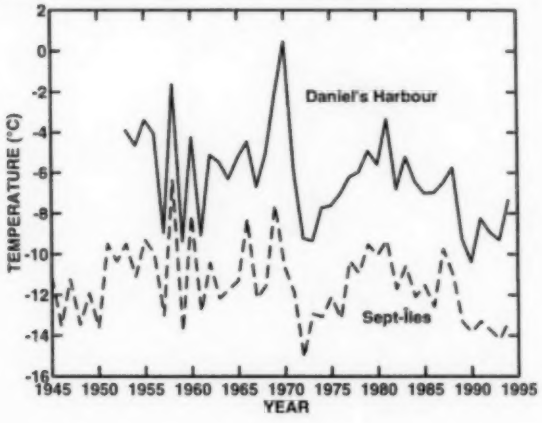
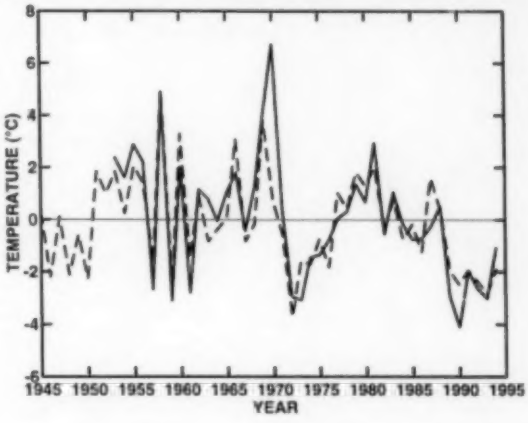


Fig. 10. Deviation from the 1961–1990 mean of the December–March average air temperature at Sept-Îles, Québec (broken line), and at Daniel's Harbour, Newfoundland (continuous line).



unimpeded local heat transfer between the ocean and the atmosphere for a large fraction of the winter season.

Conclusions and discussion

The main conclusions of our study of the Gulf of St. Lawrence CIL can be summarized as follows.

(1) The CIL is thickest, coldest, and therefore has the lowest heat content in the Northeast Gulf. At the other extreme, the CIL is warmest and has the largest heat content in Cabot Strait.

(2) The May–September warming rates of the CIL core temperature vary from 0.08°C/mo in the Central Gulf to 0.30°C/mo in the Estuary.

(3) The period from 1986 to 1994 was characterized by nine consecutive years with below-normal CIL core temperatures, seven of the eight coldest years in the entire record (47 years) occurring during this period.

(4) The midsummer CIL core temperature is positively correlated with mean air temperature from the previous winter at weather stations around the Gulf and beyond. Thus, warmer than average winter air temperatures tend to give rise to warmer than average CILs the following summer.

(5) The highest correlations of CIL core temperature with winter air temperature were obtained with weather stations from the west coast of Newfoundland: Port aux Basques (r = 0.74), Stephenville (r = 0.73), and Daniel's Harbour (r = 0.78). We argue that this is because these stations are located downstream of the Gulf of St. Lawrence relative to the dominant wind direction during the winter, so that the average winter air temperatures at these stations are in fact an indicator of the complex air–sea–ice interactions that go on over the Gulf.

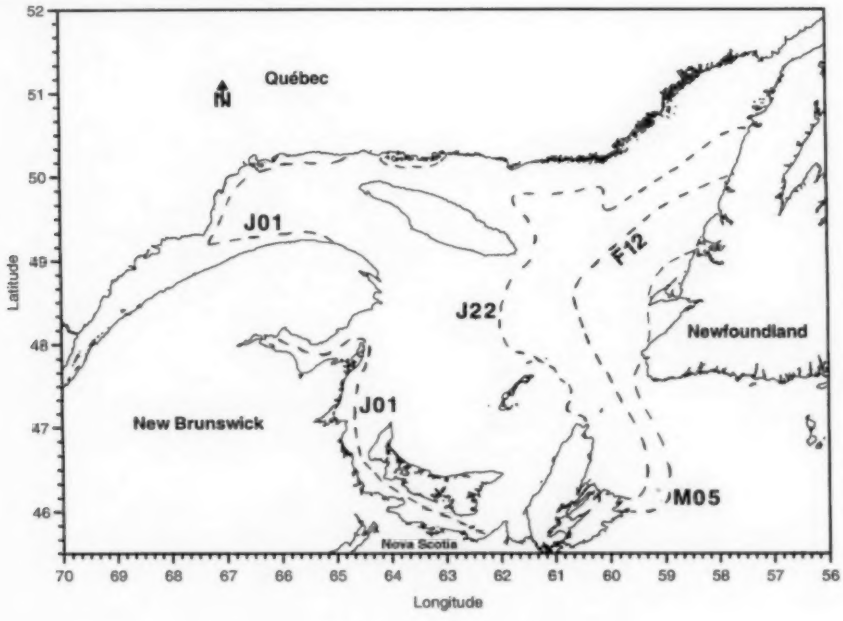
We found that the CIL is usually colder and thicker in the Northeast Gulf than in the rest of the Gulf (Fig. 5; Table 2). Three main factors could be responsible for the generally colder and thicker CIL observed during the summer in the Northeast Gulf: (*i*) inflow of water with the appropriate T and S properties through the Strait of Belle Isle, (*ii*) more intense local production of CIL waters during the winter, and (*iii*) reduced upwelling and/or vertical mixing rate, so that the CIL would get less quickly eroded in the Northeast Gulf than elsewhere during the summer. The monthly rates of change of CIL properties (Table 1) suggest that we can rule out the third factor, since the rates of change of CIL thickness, CIL core temperature, and heat content in the Northeast Gulf are similar to all other regions but the Estuary and are actually slightly greater than in the Central Gulf and Cabot Strait regions. The relative importance of the remaining two factors, in situ winter cooling of CIL waters in the Northeast Gulf itself versus advection through the Strait of Belle Isle, has not been clarified in this paper. The best estimate to date of the importance of flow through the Strait of Belle Isle (Petrie et al. 1988*b*), about 35% of the total volume of waters with $T < 0$°C and $S >$ 32 at the end of March, still remains unchallenged.

Bugden (1991) showed that the deep waters (200–300 m layer) of the Gulf of St. Lawrence are also subject to interannual and interdecadal changes of temperature with amplitudes up to about 2°C. Those changes are not related to the observed CIL variability, however (r = 0.14). This uncoupling between the CIL core temperature and the deep waters of the Laurentian Channel occurs because of the different forcing mechanisms responsible for the interannual variability in both layers. On the one hand, atmospheric temperatures and flow through the Strait of Belle Isle for a given winter are the main factors responsible for the CIL properties of the following summer (Petrie et al. 1988*b*). On the other hand, the varying proportions of Labrador and Slope waters that enter the Laurentian Channel at the shelf break, some 400 km southeast of Cabot Strait, affect the temperature, salinity, and dissolved oxygen content of the 200–300 m layer in the Gulf a few years later, the lag being a function of distance along the channel (Bugden 1991). The changes in the proportion of Labrador and Slope waters entering the Laurentian Channel may themselves be due to interannual variations in the westward transport of the Labrador Current (Petrie and Drinkwater 1993).

We did not attempt to document the interannual variability

© 1997 NRC Canada

Fig. 11. Position of the 1962–1987 median ice edge at 3-wk intervals during the period of ice cover growth: January 1 (J01), January 22 (J22), February 12 (F12), and March 5 (M05) (adapted from Côté, 1989).



of the CIL salinity for four main reasons. First, the AFAP database of temperature and salinity contains very little CTD data compared with bathythermograph and bottle data. This situation could change soon if the numerous CTD profiles from the 1980s and 1990s which are not yet part of the MEDS archive become part of an updated AFAP database of temperature and salinity. Second, temperature measurements are generally more reliable and are far more numerous than salinity measurements (Petrie 1990). Third, temperature is metabolically more important for fish than salinity, as it affects growth rates among other things. Fourth and perhaps most importantly, the depth of the core of the CIL changes seasonally as well as interannually, thus complicating the task of analyzing and interpreting the variability of the CIL core salinity, salinity being itself a function of depth.

The interannual variability of the CIL in the Gulf of St. Lawrence could have an impact on the properties of Scotian Shelf waters through the outflow of Gulf waters through Cabot Strait. Preliminary results indicate that colder than normal conditions in the 50–150 m depth range prevailed in the northeast Scotian Shelf over the last 10 yr or so (K. Drinkwater, Bedford Institute of Oceanography, Dartmouth, N.S., personal communication). Moreover, Umoh and Thompson (1994) have shown that surface forcing alone is not capable of producing a permanent CIL in Emerald Basin for instance; horizontal advection of cold water from the Gulf of St. Lawrence and/or the southern Newfoundland shelf would then play a role in the maintenance of the CIL on the Scotian Shelf. Joint field work involving scientists from the Canadian Atlantic zone is currently being planned to investigate these and other issues pertaining to the physical oceanography of the southern Newfoundland shelf, Cabot Strait, and eastern Scotian shelf area.

Acknowledgements

We thank Roger Pettipas for making the AFAP database of water temperature and salinity available to us. Ken Drinkwater described to us how this database was derived from the MEDS archive and gave us useful comments upon seeing our preliminary results at the St. John's symposium. Brian Petrie also made several suggestions that helped clarify the text. We thank Jean-François Gamache for the computer programs he wrote to allow us to perform various types of searches in the AFAP database. Jean Landry provided the CTD data from the 1987–1994 groundfish surveys in the northern Gulf, and Doug Swain provided the CTD data from the 1993 and 1994 groundfish surveys in the Southern Gulf. We are indebted to the many scientists who have contributed to the MEDS archive of temperature and salinity over the years.

References

Banks, R.E. 1966. The cold layer in the Gulf of St. Lawrence. J. Geophys. Res. **71**: 1603–1610.

Budgen, G.L. 1991. Changes in the temperature–salinity characteristics of the deeper waters of the Gulf of St. Lawrence over the past several decades. *In* The Gulf of St. Lawrence: small ocean or big estuary? *Edited by* J.-C. Therriault. Can. Spec. Publ. Fish. Aquat. Sci. **113**: 139–147.

Bugden, G.L., Hargrave, B.T., Sinclair, M.M., Tang, C.L., Therriault, J.-C., and Yeats, P.A. 1982. Freshwater runoff effects in the marine environment: the Gulf of St. Lawrence example. Can. Tech. Rep. Fish. Aquat. Sci. No. 1078.

Chouinard, G.A., and Swain, D.P. 1994. Environmental overview for the Southern Gulf of St. Lawrence in 1993. DFO Atl. Fish. Res. Doc. 94/69.

Colbourne, E. 1994. Oceanographic conditions in NAFO subdivi-

© 1997 NRC Canada

sions 3Pn and 3Ps, with comparisons to the long-term average. DFO Atl. Fish. Res. Doc. 94/26.

Colbourne, E., and Senciall, D. 1993. Temperature, salinity and density along the standard Bonavista transect. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 150.

Colbourne, E., Narayanan, S., and Prinsenberg, S. 1994. Climatic changes and environmental conditions in the Northwest Atlantic, 1970–1993. ICES Mar. Sci. Symp. **198**: 311–322.

Côté, P.W. 1989. Ice limits eastern Canadian seaboard. Environment Canada, Ottawa, Ont.

Déry, F. 1992. Interannual and intraseasonal variability of the ice cover in the Gulf of St. Lawrence, 1963–1990. M.Sc. thesis, McGill University, Montreal, Que.

Drinkwater, K.F., and Pettipas, R.G. 1993. Climate data for the Northeast Atlantic: surface wind stresses off eastern Canada, 1946–1991. Can. Data Rep. Hydrogr. Ocean Sci. No. 123.

Forrester, W.D. 1964. A quantitative temperature-salinity study of the Gulf of St. Lawrence. Bedford Inst. Oceanogr. Rep. 64-11, Dartmouth, N.S.

Gratton, Y., Pettigrew, B., Pelchat, B., Gilbert, D., Couture, M., and Landry, J. 1994. Overview of the environmental conditions in the Gulf of St. Lawrence in 1993. DFO Atl. Fish. Res. Doc. 94/55.

Koutitonsky, V.G., and Bugden, G.L. 1991. The physical oceanography of the Gulf of St. Lawrence: a review with emphasis on the synoptic variability of the motion. *In* The Gulf of St. Lawrence: small ocean or big estuary? *Edited by* J.-C. Therriault. Can. Spec. Publ. Fish. Aquat. Sci. **113**: 57–90.

Lauzier, L.M., and Bailey, W.B. 1957. Features of the deeper waters of the Gulf of St. Lawrence. Bull. Fish. Res. Board Can. **111**: 213–250.

Petrie, B. 1990. Monthly means of temperature, salinity, and sigma-t for the Gulf of St. Lawrence. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 126.

Petrie, B., and Drinkwater, K. 1993. Temperature and salinity variability on the Scotian Shelf and in the Gulf of Maine 1945–1990. J. Geophys. Res. **98**: 20079–20089.

Petrie, B., Akenhead, S., Lazier, J., and Loder, J. 1988*a*. The cold intermediate layer on the Labrador and Northeast Newfoundland shelves, 1978–86. NAFO Sci. Counc. Stud. **12**: 57–69.

Petrie, B., Toulany, B., and Garrett, C.J.R. 1988*b*. The transport of water, heat and salt through the Strait of Belle Isle. Atmos.-Ocean, **26**: 234–251.

Swain, D.P. 1993. Variation in September near-bottom temperatures in the southern Gulf of St. Lawrence, 1971–1992. DFO Atl. Fish. Res. Doc. 93/48.

Umoh, J.U., and Thompson, K.R. 1994. Surface heat flux, horizontal advection, and the seasonal evolution of water temperature on the Scotian Shelf. J. Geophys. Res. **99**: 20403–20416.

© 1997 NRC Canada

Comparison of hydrography and circulation on the Newfoundland Shelf during 1990–1993 with the long-term mean

E. Colbourne, Brad deYoung, S. Narayanan, and J. Helbig

Abstract: Meteorological and ice data from the Atlantic region indicate that the large-scale atmospheric circulation over the Northwest Atlantic during the early 1990s caused below-normal air temperatures in eastern Canada, resulting in increased ice growth during winter, increased ice transport from northern latitudes, and increased freshwater from melting ice during spring. The reduced solar flux onto the ocean surface resulted in a 3- to 4-wk delay in the annual warming cycle causing record low temperatures over the upper water column throughout the Newfoundland Shelf region. We examined temperature, salinity, and current measurements from acoustic Doppler current profilers, moored current meters, and drogued drifting buoys to establish the hydrographic conditions and circulation on the Newfoundland Shelf during 1990–1993 in relation to the longer term (1950–1989) mean. The mean circulation and transport do not show significant departures from the long-term average, but the total advective summer heat transport through the Bonavista transect indicates a 26% reduction during the early 1990s.

Résumé : Les données relatives aux conditions météorologiques et à la couverture de glace pour la région de l'Atlantique indiquent que la circulation atmosphérique à grande échelle au-dessus de l'Atlantique Nord-Ouest dans les premières années de la présente décennie a causé, dans l'Est du Canada, des températures de l'air inférieures à la normale, ce qui a entraîné une augmentation de l'englacement durant l'hiver, un accroissement du transport de glace à partir des latitudes nordiques, et une augmentation de la quantité d'eau douce provenant de la fonte des glaces au printemps. La réduction du flux solaire atteignant la surface de l'océan a entraîné un retard de 3 à 4 sem dans le cycle annuel de réchauffement, ce qui a occasionné des records de basse température de l'eau de surface, dans toute la région de la plate-forme de Terre-Neuve. Nous avons étudié les mesures de la température, de la salinité et des courants obtenues grâce à des profileurs de courant acoustiques Doppler, à des courantomètres mouillés et à des bouées dérivantes équipées de drogues, afin de déterminer les conditions hydrographiques et la circulation sur la plate-forme de Terre-Neuve au cours des années 1990–1993 par rapport aux valeurs moyennes établies sur de plus longues périodes (1950–1989). Les moyennes pour la circulation et le transport ne montrent pas d'écarts significatifs par rapport à la moyenne sur 49 ans; par contre, le transport total de chaleur par advection en été sur la section de Bonavista indique une réduction de 26% au début des années 90.

[Traduit par la Rédaction]

Introduction

The oceanographic climate on the continental shelf off eastern Newfoundland and Labrador is mainly determined by the Labrador Current, which transports cold, relatively fresh, polar water together with sea ice and icebergs from the arctic to lower latitudes along the Labrador, Northeast Newfoundland Shelf, and Grand Bank regions (Fig. 1). These arctic waters can be traced as far south as the Middle Atlantic Bight (Chapman and Beardsley 1989; and Mertz et al. 1993). The current system, which itself comprises only a small part of the circulation in the Northwest Atlantic, is formed near Cape Chidley Labrador and is fed by arctic water from the eastern arctic through Davis Strait and from Hudson's Bay and the Arctic Archipelago through Hudson Strait, reaching the Grand Bank area about 3–6 mo later (Fig. 2). The oceanic properties of the Labrador Current water over the Newfoundland continental shelf are primarily determined by meteorological wind forcing and solar heat exchange of the Northwest Atlantic including the arctic regions.

It has been suggested that environmental conditions on the shelf, either temperature (deYoung and Rose 1993) or salinity (Myers et al. 1993), strongly influence the distribution and recruitment of Atlantic cod (*Gadus morhua*). In response to the recent decline in both pelagic and groundfish resources of Atlantic Canada, there has been an increased effort to determine possible linkages to changing patterns in the physical environment. Two major research initiatives, the Northern Cod Science Program (NCSP) and the Ocean Production Enhancement Network (OPEN), yielded a large amount of environmental data from 1990 to 1993, primarily on the Northeast Newfoundland Shelf from the southern Grand Bank to Hamilton Bank on the southern Labrador Shelf (Fig. 1).

Since the late 1980s the Northwest Atlantic has experienced severe meteorological, oceanographic, and ice conditions (Drinkwater et al. 1992; Narayanan et al. 1992, 1995;

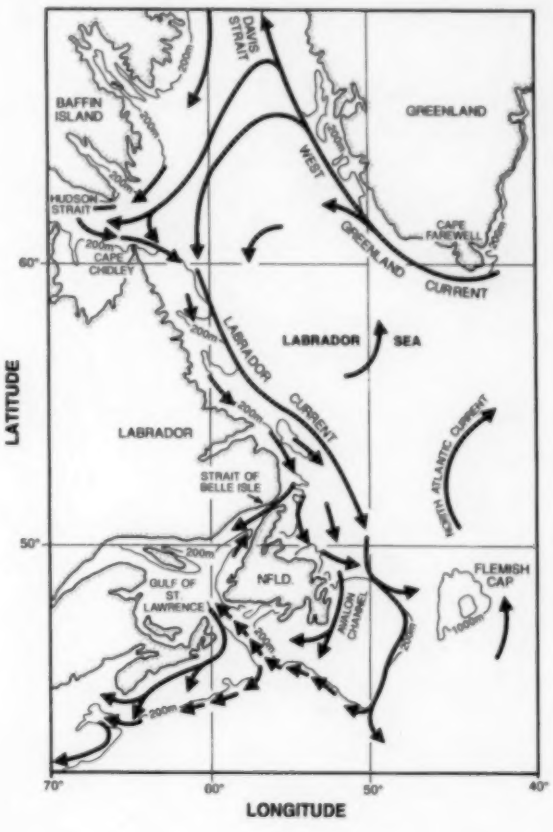
Received March 17, 1995. Accepted November 30, 1995.
J13308

E. Colbourne, S. Narayanan, and J. Helbig. Department of Fisheries and Oceans, Science Branch, St. John's, NF A1C 5X1, Canada.
B. deYoung. Physics Department, Memorial University of Newfoundland, St. John's, NF A1B 3X7, Canada.

© 1997 NRC Canada

Fig. 1. Map of the study area showing the positions of the standard Bonavista and Seal Island transects and Station 27.

Fig. 2. General circulation in the Northwest Atlantic showing major current systems (adapted from Chapman and Beardsley 1989).



Petrie et al. 1992; Drinkwater 1993; Colbourne 1993*a*; 1993*b*). In general, the continental shelf of Newfoundland and Labrador has experienced widespread negative water temperature anomalies, with upper layer temperatures reaching a record 3.0°C below normal during the early summer of 1991. In addition, salinities were generally fresher than normal during spring and summer, particularly in the upper layers where the immediate effect of the increased ice melt is felt.

The main objective of this paper is to examine how the oceanographic conditions on the continental shelf of Newfoundland and Labrador during the early 1990s have responded to the changing weather patterns. In particular, the water property distributions with reference to the long term (1950–1989) average at Station 27 and along the Bonavista transect (Fig. 1) will be reviewed. The main circulation features of the Labrador Current determined from drifting buoys, moored current meters, and ship-mounted acoustic Doppler current meters are presented. Volume and heat transports of the Labrador Current computed from historical and the 1990s data are compared with previous estimates.

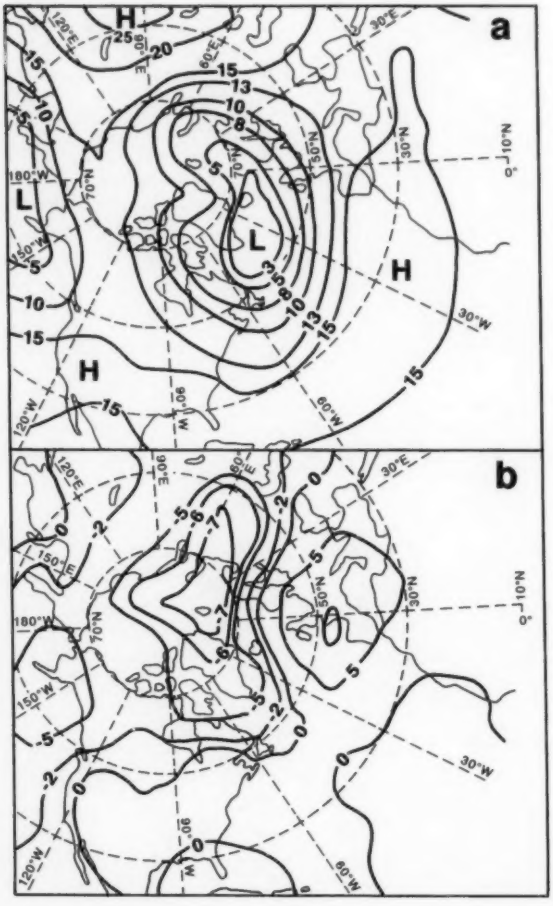
General environmental conditions

In contrast with general warming trends, 0.5°C worldwide (Jones and Wigley 1990) and 1.0°C over North America since 1900 (Saulesleja 1994), the Northwest Atlantic has experienced anomalously cold meterological conditions since the late 1980s (Findlay and Deptuch-Stapf 1991). This is a direct result of the large-scale pressure fields over the North Atlantic. A near stationary winter low pressure system centered over Iceland and a high pressure system centered over the Azores are the dominant features (Fig. 3*a*). When the Icelandic low forms during the winter months the atmospheric circulation over the region is generally from the northwest, pumping cool arctic air over large areas of the Northwest Atlantic Ocean and eastern Canada. The strength of the winter atmospheric circulation over the Northwest Atlantic is primarily influenced by the intensity of the Icelandic low which reaches its maximum during the winter months. A convenient measure of the strength of this circulation is the difference between sea level air pressure measured over the Azores and Iceland, commonly referred to as the North Atlantic Oscillation (NAO) index (Rogers 1984). Periods with high positive NAO values correspond to stronger cyclonic circulation in the North Atlantic.

During the winter months (December–February) of the early 1990s the Icelandic low was generally deeper than normal, while the atmospheric pressure over the Azores was higher than normal (Fig. 3*b*) producing a strong northwesterly circulation bringing cold arctic air to Atlantic Canada. The correlation between the 5-yr low-pass-filtered winter NAO index anomaly and the frequency of winter geostrophic winds from the northwest (315 ± 22.5°) over the Labrador Shelf is 0.75 ($p = 0.05$) (Fig. 4). As shown in the time series, particularly in the early 1990s, these circulation patterns gave rise to

© 1997 NRC Canada

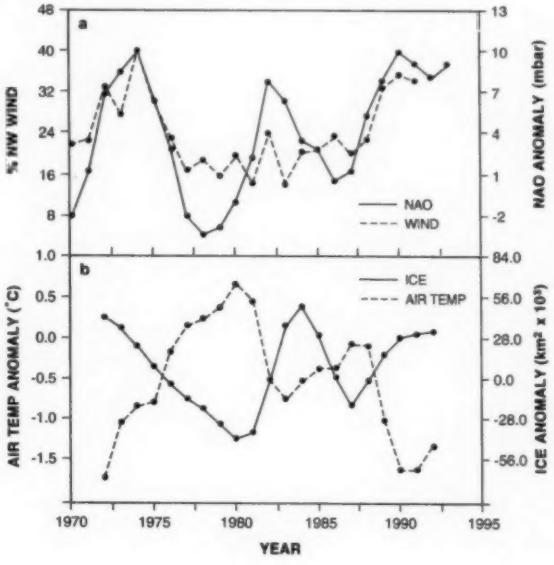
Fig. 3. (*a*) Normal (1951–1980) 100 kPa surface (decametres) pressure field over the Northwest Atlantic during winter (December–February) and (*b*) the early 1990s 100 kPa surface pressure field anomalies (courtesy of Atmospheric Environment Service, Ontario, Canada).



increased winter ice production, increased ice transport to lower latitudes, and colder than normal winter air temperatures over Atlantic Canada (Colbourne et al. 1994; Prinsenberg et al. 1997). The NAO index anomaly and Cartwright winter air temperature anomalies and the Northeast Newfoundland Shelf ice coverage anomalies are all significantly correlated (r = –0.85 and 0.72 (p = 0.05), respectively).

The oceanographic conditions on the Newfoundland Shelf have responded in phase with the meteorological and sea ice anomalies discussed above. The cross-sectional area of subzero (Celsius) water (cold intermediate layer, CIL) on the continental shelf off Cape Bonavista (Fig. 5*a*) shows an increasing trend from the early 1970s to the present, with large-amplitude fluctuations at near decadal time scales which are highly correlated with the meteorological and ice conditions (e.g., r = 0.78, p = 0.05 for CIL and ice anomalies). Similarly, the total heat content ($H/c_p\rho$) of the water column at Station 27 (Fig. 5*b*) correspondingly decreased during

Fig. 4. Time series of the (*a*) 5-yr averaged NAO index anomaly (1 mbar = 100 Pa) and frequency of winter northwesterly winds at Cartwright, Labrador, and (*b*) air temperature anomalies at Cartwright and ice coverage anomalies over the Newfoundland Shelf between 49 and 52°N (adapted from Colbourne et al. 1994).



the same time period, again with large-amplitude fluctuations at near decadal time scales. The total heat content of the water column at Station 27 reached record lows during the early 1990s.

Data

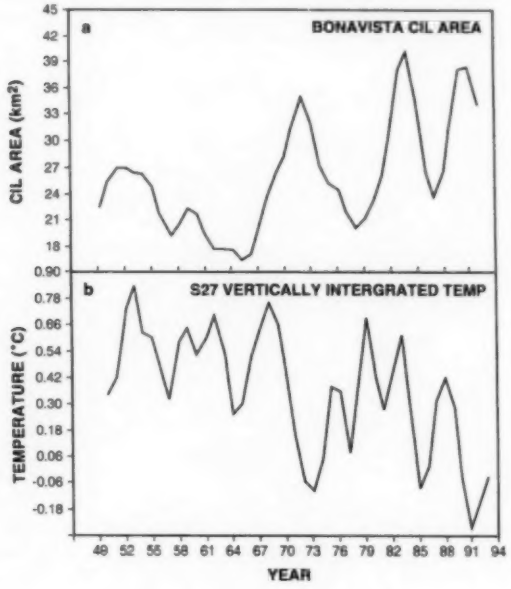
Temperature and salinity

Extensive monitoring of environmental conditions on the Northeast Newfoundland Shelf was initiated under the NCSP and OPEN initiatives during the early 1990s. Vertical profiles of temperature and salinity data were collected using several different conductivity–temperature–depth (CTD) recorders including Neil Brown MKIIIB and Seabird SBE-19s, SBE-25s, and SBE-911s. Factory and frequent field calibrations maintained accuracies of 0.005°C for temperature and 0.005 for salinity. In addition, an extensive amount of historical data was available for the Newfoundland Shelf area from the Marine Environmental Data Service (MEDS) in Ottawa, Ont., Canada, and from archives at the Northwest Atlantic Fisheries Centre (NAFC) in St. John's, Nfld., Canada.

Before the late 1970s, most temperature and salinity data were collected at standard depths using water sampling bottles fitted with reversing thermometers. Since the 1960s and up to the present, a considerable amount of data was also collected using mechanical and electronic bathythermographs, but since the late 1970s, CTD recorders have been the standard. The data were quality controlled for obvious spikes, range restricted and linearly interpolated or decimated if necessary to 5.0-m depth intervals. The profiles were not extrapolated beyond their depth range.

© 1997 NRC Canada

Fig. 5. Time series of the (*a*) summer CIL cross-sectional area of water temperature less than 0.0°C from 1948 to 1993 and (*b*) Station 27 vertically (0–176 m) integrated temperature time series.



Currents

Extensive monitoring of the water currents on the Northeast Newfoundland Shelf and Hamilton Bank off southern Labrador during the early 1990s was done using satellite-tracked drifting buoys, moored current meters, and vessel-mounted acoustic Doppler current profilers (ADCPs).

Forty-nine drifting buoys were deployed on or near Hamilton Bank during the NCSP during 1991 and 1993 at various times from summer to fall near Hamilton Bank and the continental shelf in five separate clusters about 20 and 60 km in diameter. The buoys were spar shaped with a total length of 1.0 m and a maximum diameter of 0.5 m. Each buoy was fitted with a weighted 0.8-m diameter, 10-m-long holey sock drogue that was suspended between 15 and 25 m in the water column. The ratio of holey sock area to that of the buoy hull and tether was about 43:1, ensuring that the difference between the true "surface" current and the buoy speed was at most a few centimetres per second. Their positions were determined by the System Argos satellite service which provided, on average, about eight position fixes per day for each drifter.

Buoy, and hence surface, velocities were determined by fitting a B-spline to the individual observations, each of which was weighted by the estimated positional accuracy provided by System Argos. Positions and velocities were interpolated to a 3-hourly interval. These tracks were then passed through a fifth-order Butterworth lowpass filter designed to eliminate variability at temporal scales less than 24 h, thereby removing most of the tidal and inertial energy.

The ADCPs used were vessel-mounted 153.4-kHz systems manufactured by RD Instruments. These units employed four transducers mounted at 30° to the vertical and 90° in the azimuth. During all measurements, the ADCPs were operated in bottom-track mode on the continental shelf with a bin depth of 4.0 m and a sampling interval of 5.0 min, corresponding to a spatial along-track resolution of approximately 1.5 km. The number of depth bins was set to 75 corresponding to a depth range of 300 m, about the maximum useful range of the ADCP at this frequency and deep enough to reach close to bottom over most of the continental shelf. The bottom-tracking range of the 153.4-kHz system was between 500 and 600 m, depending on the sea state conditions and vessel operating speeds. Valid data were obtained from about 12 m depth to within 85% of the bottom in water depths less than 300 m and to about 300 m in water depths up to a maximum of 600 m. Data were also collected in deeper water beyond the bottom-tracking range but not included in the analysis here due to the lack of an accurate reference. The data were manually edited to remove invalid ensembles resulting from ship motion and then despiked using a threshold of 0.10 m/s on the error velocity (Colbourne et al. 1993). Invalid bins were then two-dimensionally linearly interpolated. Each transect was then filtered using a two-dimensional cosine bell filter of length 12 m vertically by approximately 5 km horizontally.

The moored current meters were Aanderaa RCM 5s and 7s and InterOcean S4s sampling at either 0.5- or 1.0-h intervals. Current meter moorings were deployed starting in the summer of 1990 and continued to 1994 in the inshore, midshelf, and the outer shelf areas in water depths ranging from 40 to 900 m (Narayanan 1994). Data recorded by these instruments included speed and direction, and, whenever possible, temperature, conductivity, and pressure. Data from approximately the same depth and location were concatenated and low-pass filtered using Godin's tide-removing filter (Godin 1972). The data were then subsampled at 6-hourly intervals. The processed time series were then used to compute statistics for the entire sampling period, including u and v components, standard deviations, and extremes.

Water property distributions

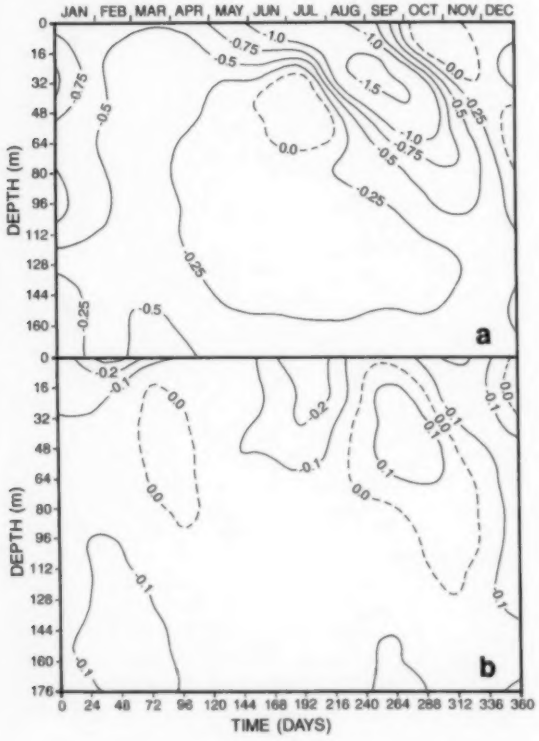
Station 27

Station 27 is a standard hydrographic monitoring station in the inshore branch of the Labrador Current on the continental shelf established in 1946 (Templeman 1975). It is located about 8 km off St. John's Harbour, Newfoundland (Fig. 1), in a water depth of 176 m. This position is ideal for monitoring the inshore branch of the Labrador Current, since the cold water (<0.0°C) that forms the CIL on the continental shelf is present year-round in depths from about 100 m to the bottom at 176 m depth. In recent years, this station has been occupied on a regular basis, about two to four times per month, making it one of the most frequently monitored hydrographic stations in the Northwest Atlantic. This regular sampling permits a detailed analysis of the seasonal and interannual variability in the core of the CIL as well as the upper layer conditions on the inner Newfoundland Shelf.

As presented in Colbourne et al. (1994) and following the general methods of Smith (1983), Akenhead (1987), and Myers et al. (1990) the seasonal cycles in temperature and salinity fields were determined by fitting a least-squares regression of the form $\cos(\omega t - \phi)$ to the data. The time series of temperature and salinity anomalies presented in Colbourne et al. (1994) showed a high degree of variability, par-

© 1997 NRC Canada

Fig. 6. Monthly time series of (*a*) temperature and (*b*) salinity anomalies as a function of depth at Station 27 during the period 1990–1993 referenced to a 1950–1989 average.



ticularly in the upper water column with fluctuations of ±2.0°C and 1.0 psu at periods of about 1 yr. Variations in the anomalies near the bottom appear to have roughly a decadal time scale similar to that of the NAO index.

The vertical distribution of temperature anomalies during the early 1990s (Fig. 6*a*) referenced to the 1950–1989 mean shows winter temperatures ranging from 0.25 to 0.75°C below normal throughout the water column. The anomalies range from 0.5 to 1.5°C below normal during spring and summer in the upper water column and from 0.25 to 0.5°C below normal throughout the time period near bottom. During the early 1990s, upper layer water temperatures reached the lowest values ever recorded off St. John's (3.0°C below normal at 30 m depth during early summer of 1991), while the bottom temperature has remained below normal at about 0.5–1.0°C since 1986, the longest period since measurements began in 1946.

Similarly the vertical distribution of salinity anomalies (Fig. 6*b*) shows slightly fresher than normal conditions (generally by about 0.1–0.2 psu) in the upper water column during the winter and summer months and slightly saltier conditions during September and October due to a phase shift in the annual cycle compared with the long-term mean. Normally the salinity at Station 27 reaches its minimum during late September, corresponding to the arrival of spring ice-melt water from the Labrador Shelf (Myers et al. 1990). During the early 1990s, this was probably delayed due to the delayed spring warming.

These colder and fresher oceanographic anomalies are highly correlated with the large-scale atmospheric circulation, lower air temperatures, increased ice cover, and more frequent northwest winds, particularly during the early 1970s and 1990s and to a lesser extent the mid-1980s (Fig. 4). For example, the correlation between lower than normal air pressure over Iceland (i.e., positive NAO index anomaly) and bottom water temperature anomalies at Station 27 is –0.7 ($p = 0.05$).

Bonavista temperature and salinity

The Bonavista transect located between the Northern Grand Bank and the Southern Funk Island Bank (Fig. 1) has been occupied on a regular basis since 1950 (Colbourne and Senciall 1993). The station positions of all observations in a corridor with boundaries at ±25′ latitude along the transect, for the purposes of this analysis, were assumed to lie along a straight line with offshore distance calculated from Cape Bonavista. The data were then projected onto a 5.0-km horizontal by 5.0-m vertical grid and a simple arithmetic mean computed.

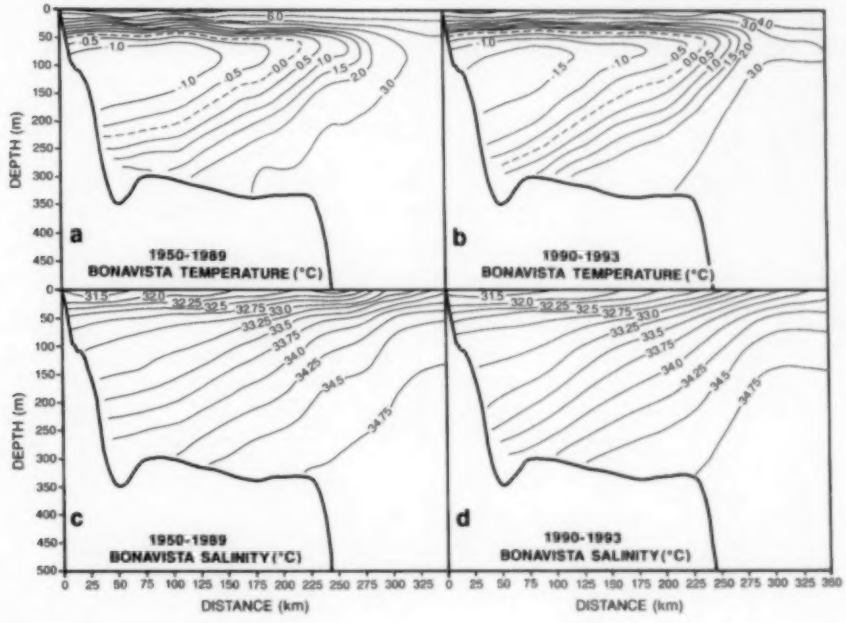
A dominant feature of the summer temperature structure on the continental shelf of eastern Canada is the large volume of subsurface water with temperatures ranging from 0.0°C to near freezing at –1.84°C, commonly referred to as the CIL (Petrie et al. 1988), and the strong temperature front separating the warmer slope water from the Labrador Current water (Narayanan et al. 1991). This feature extends from below the mixed layer at about 50 m depth to near the bottom over the outer portion of the shelf. In the winter months, the warm surface layer disappears as it cools down to near freezing temperatures due to winter cooling and strong surface mixing from winter storms. During spring and summer, ice melt and seasonal heating increase the stratification in the upper layers trapping a cold layer of water confined to the continental shelf between the warm surface water and the warmer slope water near the bottom.

The mean offshore extent of the Cape Bonavista (Fig. 7*a*) CIL for 1950–1989 was about 220 ± 44 km, centered at approximately 100 m depth with a mean thickness about 200 ± 35 m (Colbourne et al. 1994). The CIL cross-sectional area corresponding to the 1990–1993 average was 37 km^2 compared with the long-term value of 26.4 ± 8.7 km^2. In the nearshore regions during the summer months, water above 0.0°C is mainly restricted to the upper 50 m of the water column extending to less than 20 km offshore near the bottom. In deeper water, a strong across-shelf gradient (≈0.02°C/km) exists, with temperatures increasing from 0.0°C at 225 m depth to 3.0°C at the shelf break. During the early 1990s, summer temperatures in the upper layer were up to 2.0°C below average and up to 0.5°C below average in the core of the CIL (Fig. 7*b*). In addition, subzero (Celsius) water was much more extensive during the 1990s, reaching further offshore and deeper into the water column over the continental shelf.

The summer salinity (and hence density at these temperatures) structure on the shelf (Figs. 7*c* and 7*d*) shows a strong horizontal gradient indicated by the net upward displacement of the isohalines towards the offshore. The salinities during the early 1990s ranged from 0.1 to 0.2 psu below normal over the shelf as indicated by the general depression of the isohalines. Beyond the shelf break (>250 km offshore), salinities were near to slightly above normal.

© 1997 NRC Canada

Fig. 7. Vertical cross-section of the (*a* and *b*) temperature and (*c* and *d*) salinity fields along the standard Bonavista transect for the periods 1950–1989 and 1990–1993.



Continental Shelf bottom temperatures

The average near bottom temperature over most of the Northeast Newfoundland Shelf for the period 1950–1989 ranged from about –1.0 to 0.0°C inshore to greater than 3.0°C at the shelf break in water depths of 500 m or more (Fig. 8*a*). The average temperature over most of the Grand Bank ranged from less than –0.5 to 3.0°C at the edge of the bank. In general, bottom temperatures on the continental shelf are strongly influenced by the local bathymetry, with isotherms exhibiting mainly east–west gradients over most areas (Colbourne and Foote 1994; deYoung et al. 1994). These maps were constructed by contouring the temperature value at the bottom of each profile for each time period. If the bottom of the profile was not within 90% of the total water depth the profile was rejected from the analysis.

The bottom temperatures during the early 1990s have been significantly below average over the entire area. For example, the percentage area of sub-zero (Celsius) water on the Grand Bank during the period 1990–1993 was significantly larger than the 1950–1989 average (Fig. 8*b*). In general, during the early 1990s the bottom temperatures over most of the Grand Bank ranged from 0.25 to 1.0°C below the 1950–1989 average. In water depths greater than 200 m, bottom temperatures have been near normal throughout the region.

Labrador Current

General circulation

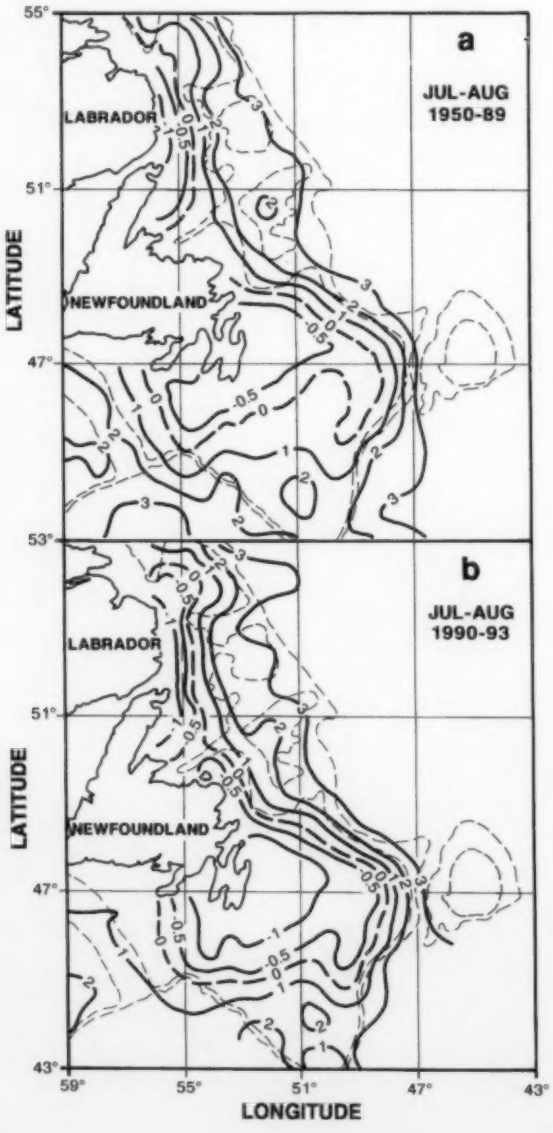
The circulation in the Northwest Atlantic (Fig. 2) has been described many times (Smith et al. 1937; Peterson 1987; Greenberg and Petrie 1988; Lazier and Wright 1993; Petrie and Anderson 1983). It consists of the west Greenland Current which flows around Cape Farewell and up the west coast of Greenland, a branch of which turns and crosses the northern Labrador Sea forming the northern section of the Northwest Atlantic subpolar gyre. Near Cape Chidley, outflow through Hudson Strait combines with the east Baffin Island Current and a part of the west Greenland Current to form the western section of the gyre. This current then flows down the Labrador coast as a strong western boundary current known as the Labrador Current. A component of the current follows the various cross-shelf saddles on the Labrador coast forming a well-defined inshore branch by the time the current reaches Hamilton Bank with average speeds of approximately 0.15 m/s carrying about 15% of the total transport. Most of the flow remains bathymetrically trapped at the edge of the continental shelf with average speeds of approximately 0.40 m/s carrying about 85% of the total transport mainly between the 400- and 1200-m isobaths (Lazier and Wright 1993). Further south, near the northern Grand Bank, the inshore branch becomes broader and less defined with most of the transport combining with the offshore branch and a part which flows through the Avalon Channel around the Avalon Peninsula westward along the Newfoundland south coast. The offshore branch flows around the tail of the Grand Bank westward along the continental slope, where it is influenced by the Gulf Stream and slope waters, to the Laurentian Channel and into the Gulf of St. Lawrence (Hachey et al. 1954). Additionally, part of the flow combines with the North Atlantic Current and forms the southern section of the subpolar gyre.

Velocities, mean flows, and transport

The Labrador Current consists of a baroclinic component as well as a barotropic component. The relative baroclinic component perpendicular to a transect can be calculated from the density field determined by temperature salinity and pressure

© 1997 NRC Canada

Fig. 8. Summer (July–August) continental shelf horizontal bottom temperature maps for the 1950–1989 (*a*) and (*b*) 1990–1993 averages.



measurements, assuming a balance between the Coriolis force and the horizontal pressure gradient. The total current, baroclinic plus barotropic, can be measured using moored current meter arrays, ship-mounted ADCPs, and satellite-tracked Lagrangian drifters.

Drifter, ADCP, and current meter observations

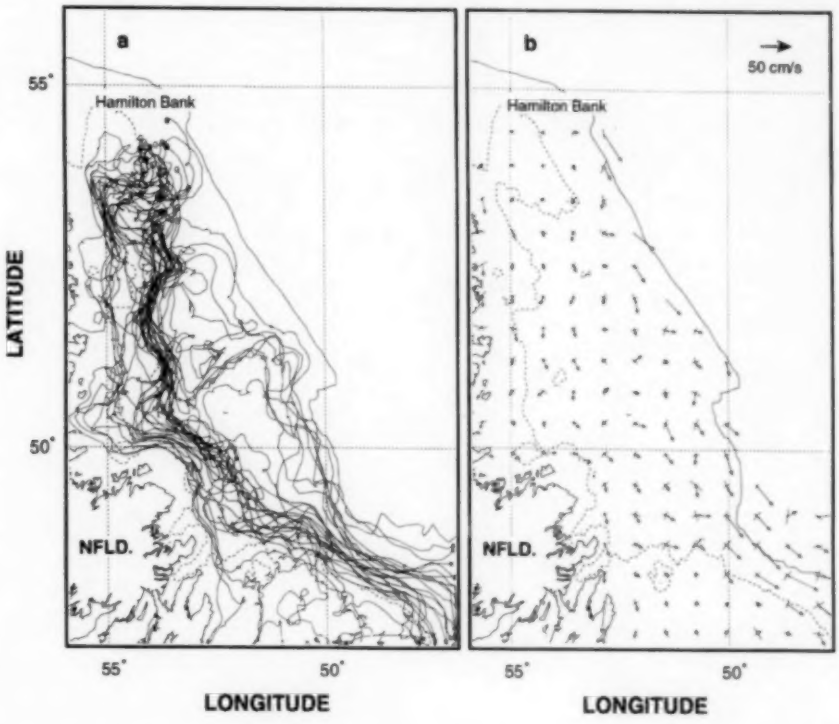
The 49 drifting buoy tracks were used to derive a mean upper layer flow field for the Northeast Newfoundland Shelf. All buoys were deployed inshore of the 600-m isobath in an effort to avoid the offshore branch of the Labrador Current, since these drifter deployments were designed to simulate the drift of fish eggs and larvae on the shelf. The buoys generally moved in a southerly direction and displayed a remarkably consistent drift onshore through Hawke Saddle south of Hamilton Bank (Fig. 1) and remained over the shelf until they joined the offshore branch of the Labrador Current along the northern edge of the Grand Banks through the Bonavista Corridor (Fig. 9*a*). The buoys also tended to sample certain regions preferentially: areas where currents diverge were undersampled whereas buoys tended to cluster in convergence zones. Also noteworthy are the few buoys that grounded inshore as well as those (six) that drifted onto the northern Grand Bank or into the inshore branch of the Labrador Current. A significant portion of the buoys released on Hamilton Bank followed the broad inshore branch of the Labrador Current over the Northeast Newfoundland Shelf until most were bathymetrically funnelled offshore through the Bonavista Corridor (Fig. 1) where they were entrained in the offshore branch. The small number that arrived on the Grand Bank indicates that the inshore branch is very broad and weak south of the Bonavista transect with the exception of some nearshore intensification through the Avalon Channel. Thus the retention of ichthyoplankton on the Grand Bank may be less influenced by the Labrador Current than elsewhere on the Newfoundland Shelf considering the longer residence time of Grand Bank waters (Helbig et al. 1992).

To produce the velocity field from the drifting buoys, the data were spatially binned into 50-km squares and then a track-length weighted average was produced. Where currents are relatively strong, the mean velocities tend to be large compared with fluctuations, but over the shelf, where mean currents are relatively weak, fluctuations and mean velocities are of similar magnitude (Fig. 9*b*). To compare the means and standard deviations of the currents derived from the drifting buoys with the moored instruments, we extracted the current vectors corresponding to those bins that contain a current meter mooring, which was typically at 40 m depth. In general, the drifting-buoy-derived near-surface currents are similar in direction to those monitored at 40 m by the fixed current meters (Fig. 10), but the fluctuations are considerably more energetic, with standard deviations often larger than the means (Table 1). This is not unexpected, since a drogue at 15–25 m depth will experience high-frequency surface effects stronger than at 40 m depth. The average magnitude of the currents derived from drifter tracks over the depth range of 15–25 m is 0.175 m/s compared with 0.102 m/s from the current meters at 40 m depth, a ratio of 1.7. This is consistent with the ratio of the International Ice Patrol (IIP) composite of all available upper layer current information to subsurface current meter measurements at 40 m depth (Narayanan et al. 1996). In general, these results show a strong offshore branch of the Labrador Current with low variability, while the currents over the banks tend to be weaker with high variability. Most of the variability over the shelf occurs in the weather band (≈2–10 d) (Narayanan 1994; Fissel and Lemon 1991) from wind-driven circulation due to storms and eddies at internal Rosby radius scales (≈10 km on the shelf).

Current measurements made along transects from moving vessels using ADCPs include the high- frequency weather band components, eddies, and tides. The removal of tides from ADCP data collected on moving platforms is difficult.

© 1997 NRC Canada

Fig. 9. (*a*) Low-pass-filtered drifting buoy tracks. Drop locations are indicated by circles and terminal positions by asterisks. (*b*) Spatially binned mean surface currents derived from spatial averages of all drifting buoy tracks. The principal axes of variation are indicated by crosses.



Unlike time series of current measurements obtained from fixed sites, ADCP measurements obtained from moving platforms do not lend themselves to a simple harmonic analysis, since the amplitude and phase of the tidal components vary spatially along the transect. In an attempt to approximate the mean flow from our ADCP measurements, we averaged the along-shelf (–30° from north) components from about 40 transects. These measurements were made along the east coast of Newfoundland on more than a dozen surveys at various times from May to November from 1991 to 1993 within about 30′ latitude of the standard Bonavista transect (Fig. 1). The current field revealed by these data does not show distinct inshore and offshore branches of the Labrador Current but rather a continuously increasing current speed from 0.05 to 0.10 m/s nearshore to over 0.20 m/s at the shelf edge (Fig. 11). The high-frequency variability has been smoothed by the averaging procedure. There is close agreement between the fixed current meter and average ADCP measurements in the offshore and midshelf areas, but the two differ by a factor of 2 nearshore in the upper 100 m of the water column. In this region the fixed current meter measurements are higher than the averaged ADCP measurements. It should be noted that the averaging periods for the two data sets do not correspond exactly.

Geostrophic circulation and transport

The historical (1950–1989) and recent (1990–1993) summer (July and August) temperature and salinity data along the Seal Island and Bonavista transects (Fig. 1) were averaged into 5.0 km by 5.0 m bins as described above and used to calculate the steric height along each transect from (Gill 1982)

$$\Phi = \int_0^p \delta \, dp$$

where p is the pressure or depth and δ is the specific volume anomaly given by

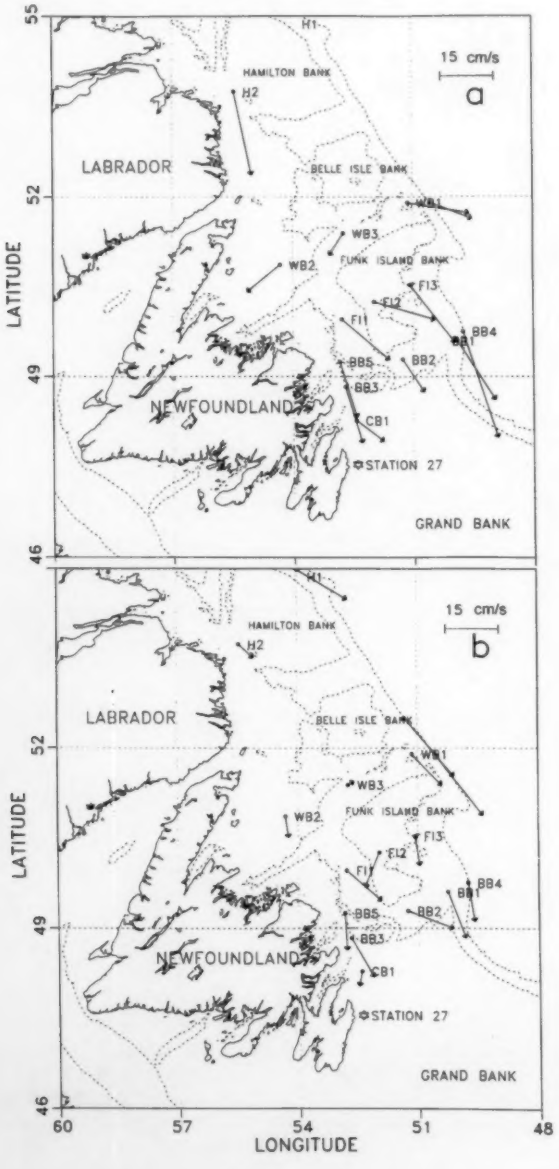
$$\delta = \alpha(s, t, p) - \alpha(35, 0, p)$$

and $\alpha = \rho^{-1}$. The geostrophic velocity between adjacent horizontal bins is then calculated from the horizontal gradient of Φ using the geostrophic balance relationship. Calculating the geostrophic velocity from the average density field for the two time periods rather than from individual density profiles for each year will produce a smoothed velocity field, but the transport will be representative of the average conditions.

The geostrophic currents relative to 500-m along the Seal Island transect for the two averaging periods show a weak inshore branch within 100 km from the shore and a much stronger offshore branch about 100 km wide centered at about 220 km offshore over the 500-m isobath (Figs. 12*a* and 12*b*). In the offshore branch, current speeds range from 0.05 m/s at 200 m depth to greater than 0.30 m/s in the upper 30 m of the water column near the edge of the continental shelf. In the inshore branch, current speeds are generally less than 0.10 m/s and near 0.0 m/s over midshelf on Hamilton Bank.

© 1997 NRC Canada

Fig. 10. (*a*) Near surface current vectors derived from the drifting buoys at the mooring locations and (*b*) average current vectors from the top current meter.



The geostrophic currents relative to 300 m depth along the Bonavista transect for the two averaging periods reveal an offshore branch as a narrow bathymetrically trapped jet near the edge of the continental slope. The offshore feature is about 75 km wide with speeds ranging from 0.05 m/s at 200 m depth to greater than 0.30 m/s in the upper 50 m of the water column (Figs. 12*c* and 12*d*). The inshore branch along the Bonavista transect appears broad and less well defined compared with upstream conditions along the Seal Island transect, with typical current speeds less than 0.10 m/s. This is also evident in the summer density field along the standard Bonavista transect (Fig. 7) and in the Seal Island transect data (Colbourne et al. 1995).

The transport (T) for both transects was calculated by integrating vertically through the water column using a bin size of 5.0 m and horizontally in the offshore direction across the shelf using a bin size of 5.0 km from

$$T = \int_0^L \int_{-h}^0 V \, dp \, dx$$

where L is the total horizontal distance across the shelf, V is the current speed perpendicular to the transect and h is the reference level, p is the pressure or depth, and x is the cross-shelf distance.

The geostrophic transport calculated through the Seal Island transect is about 3.5 Sv (1 Sv = 10^6 m^3/s) for the 1950–1989 average and 4.2 Sv for the early 1990s compared with 3.8 Sv calculated by Lazier and Wright (1993) for the period 1978–1987, referenced to 1500 m. The geostrophic transport through the Bonavista transect is about 3.1 Sv with no significant difference between the two averaging periods. The total transport calculated from the bottom-tracked ADCP data is about 6.0 Sv. It should be noted here, however, that a significant portion of the offshore branch was not included due to the lack of a reference. Therefore, this estimate does not represent the total transport of the Labrador Current.

The total current field (Fig. 13) (i.e., barotropic plus baroclinic components) through the Bonavista transect for the period 1990–1993 was determined by referencing the geostrophic currents (Fig. 12*d*) to the ADCP measurements (Fig. 11) at approximately 300 m depth across the shelf. The reference currents beyond the bottom-tracking range of the ADCP (500–600 m) were linearly extrapolated based on the last several bottom-tracked ensembles. The total transport calculated from this current field is 11.9 Sv compared with 11 Sv calculated by Lazier and Wright (1993) through the Seal Island transect based on data collected from 1978 to 1987. They estimated a barotropic component of approximately 7.2 Sv from current meter measurements made close to the bottom along the 1000-m isobath at the edge of the shelf and assuming a horizontal structure for the barotropic component similar to the horizontal structure of the surface current.

The results presented here do not show significant differences in the geostrophic transport of the Labrador Current during the most recent cold period of the early 1990s compared to that for period 1950-1989. This is in contrast with the results obtained by Myers et al. (1989) who showed a significant negative correlation between the upper layer (top 100 m) geostrophic transport along the Seal Island transect and the NAO index indicating reduced transport during cold periods. In addition, Petrie and Drinkwater (1993) suggested that increased transport of Labrador Current water around the southeast Grand Bank during warm periods (mid-1960s) on the Northeast Newfoundland Shelf resulted in colder conditions on the Scotian Shelf. In our analysis, we averaged all data during the period 1950–1989 which included the two major cold periods of the early 1970s and mid-1980s (Colbourne et al. 1994); thus, we may have averaged out some interannual trends in the transport. Moreover, our geostrophic transport estimates were referenced to 300 m which may not

© 1997 NRC Canada

Table 1. Comparison of the top current meter (CMS) measurement of the u and v components and the standard deviations of the Labrador current with the estimate derived from the drifting buoys (Drifters) for the same location (see Fig. 10 for station locations).

	Position		CMS (cm/s)				Drifters (cm/s)			
Stn.	Lat.	Long.	u	σ_u	v	σ_v	u	σ_u	v	σ_v
BB1	49°36.0′	50°15.2′	5.1	4.4	−13.4	7.7	11.1	15.8	−17.5	24.6
BB2	49°17.0′	51°15.5′	13.2	7.6	−5.0	6.1	6.2	15.0	−9.3	16.5
BB3	48°50.0′	52°41.0′	6.5	8.3	−11.4	7.5	4.9	9.8	−16.4	18.0
BB4	49°45.0′	49°45.0′	1.8	1.6	−11.0	4.7	10.3	15.7	−32.0	35.6
BB5	49°15.0′	52°50.0′	0.5	8.0	−10.7	6.8	4.9	9.8	−16.4	18.8
CB1	48°16.4′	52°25.6′	−0.7	7.6	−3.7	5.8	7.8	11.3	−5.8	12.0
F11	49°57.0′	52°47.0′	10.1	5.8	−8.7	5.6	14.1	18.2	−12.0	16.2
F12	50°15.0′	51°58.0′	−4.1	4.0	−9.9	4.8	18.2	20.5	−5.3	10.1
F13	50°31.0′	51°4.0′	1.3	5.8	−8.1	7.4	13.4	19.4	−17.3	25.2
WB1	51°54.0′	51°8.0′	8.6	10.3	−9.1	6.8	18.2	22.7	−3.1	17.0
WB3	51°23.0′	52°44.0′	1.1	3.5	0.7	3.1	−3.9	11.1	−6.1	11.5
SP2	51°54.0′	50°34.0′	14.2	5.8	−18.4	7.6	12.2	14.5	−4.7	10.6
WB2	50°51.5′	54°18.5′	0.8	2.4	−5.7	6.3	−9.7	16.0	−7.8	12.6
H1	54°59.0′	53°58.7′	14.8	8.9	−8.7	5.6				
H2	53°44.5′	55°26.9′	3.9	5.6	−3.6	5.8	5.2	8.2	−25.0	25.9

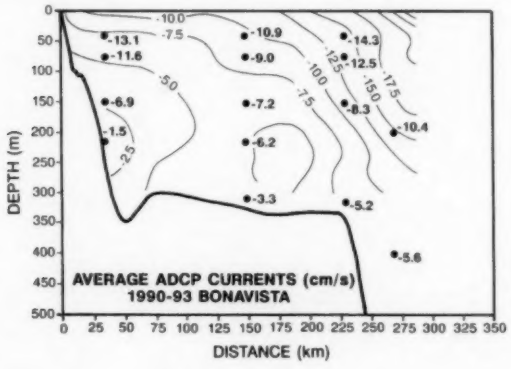


Fig. 11. Average current field derived from about 40 bottom-tracked ADCP transects collected along and near the standard Bonavista transect between 1990 and 1993 with the current meter means superimposed.

be as sensitive to upper layer changes in the stratification resulting from interannual variations in the meteorological forcing as would, for example, the transport referenced to 100 m depth.

The cumulative volume transport (Fig. 14) across the shelf along the Bonavista transect increases in the offshore direction almost linearly on the shelf (within ≈200 km from Cape Bonavista), consistent with the broad inshore branch of the Labrador Current shown earlier in that area. The total transport is about 2.5 Sv within 150 km off the shore with a baroclinic component of about 1.5 Sv. This represents approximately 20% of the total transport that we calculated along this transect, not inconsistent with the generally accepted 15% for the inshore branch. There is also some indication that higher geostrophic transport occurred over the shelf during the early 1990s compared with 1950–1989, probably due to stronger horizontal density gradients caused by the increased freshwater from the melting ice cover on the continental shelf during the spring. It should be noted that the total transport computed here is that due to the portion of the Labrador Current over the continental shelf and slope regions perpendicular to the CTD transect. The flow in this region, however, has a significant cross-shelf component as indicated by the tracks from the drifting buoys (Fig. 9). Furthermore the Labrador Current is part of the much larger Northwest Atlantic subpolar cyclonic gyre which extends into the Labrador Sea with a total transport approaching ≈40 Sv (Leetmaa and Bunker 1978).

Heat transport

The temperature structure on the shelf is determined in part by the advective heat flux from upstream. In this section, we calculate and compare the total advective summer (July–August) heat transports through the Bonavista transect for the periods 1950–1989 and 1990–1993. Since no significant difference in the geostrophic transport was found between the two averaging periods, we will base these estimates on the total volume transports calculated in the previous section for the period 1990–1993, i.e., the geostrophic flow referenced to the ADCP measurements at 300 m depth (Fig. 13). By using the same velocity field for the two periods, we will only detect differences in heat transport caused by differences in the temperature field alone (Figs. 7*a* and 7*b*). Hence the differences in the heat transport due to any variability in the volume transport between the two time periods will not be detected. The heat transport (H) through a vertical cross section in watts may be approximated from (Bryan 1962)

$$H = \rho\, c_p \int_0^L \int_{-h}^0 V\, T\, dp\, dx$$

where ρ is the average density taken as 1025 kg/m^3, c_p is the average specific heat of seawater at atmospheric pressure,

© 1997 NRC Canada

Fig. 12. Vertical cross-sections of the geostrophic currents along the (*a* and *b*) standard Seal Island and (*c* and *d*) Bonavista transects for the periods 1950–1989 and 1990–1993.

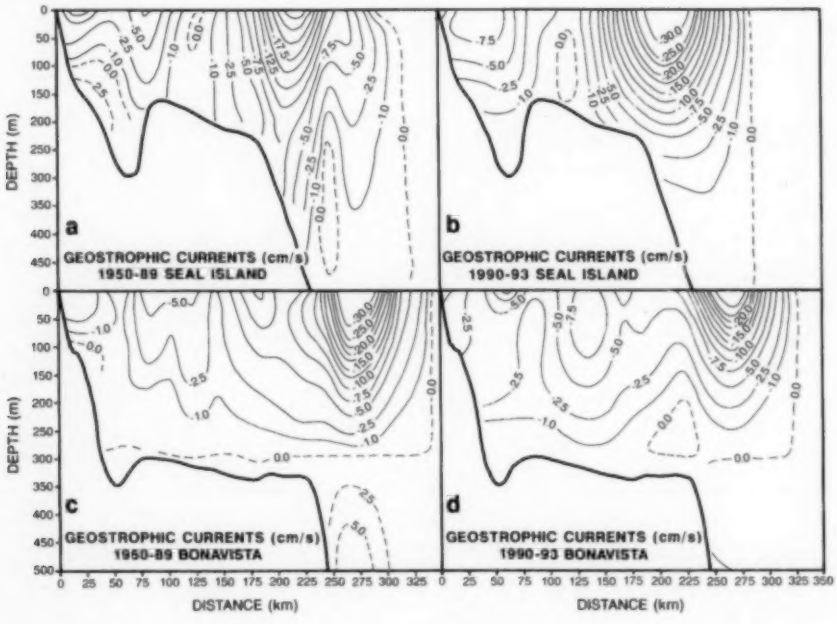


Fig. 13. Vertical cross-section of the total current field along the standard Bonavista transect for the period 1990–1993, obtained by referencing the geostrophic currents to the ADCP measurements at 300 m depth. The current meter means are superimposed.

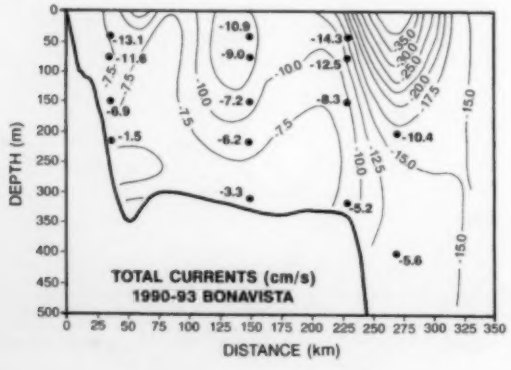
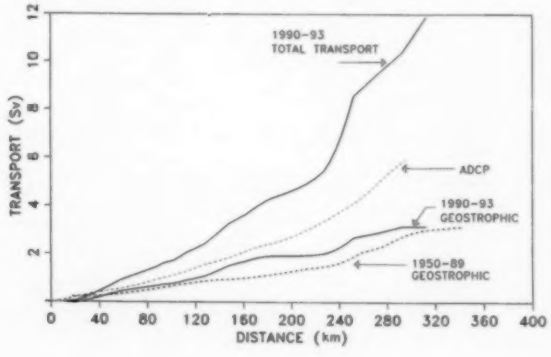


Fig. 14. Cumulative 1990–1993 total transport, 1950–1989 and 1990–1993 geostrophic transports, and the transport from the ADCP measurements along the Bonavista transect. The horizontal distance is from Cape Bonavista in the offshore direction.



about 4000 $J \cdot kg^{-1} \cdot °C^{-1}$ at 0.0°C and 33.5 psu salinity (Millero et al. 1973), T is the temperature (degrees Celsius), V is the current speed in (metres per second) perpendicular to the transect, p is the pressure or depth along the transect, and x is the cross-shelf distance.

The atmosphere–ocean heat flux Q exhibits a strong annual cycle with a heat loss of the order of –75 W/m^2 during the winter months to a heat gain of over 200 W/m^2 during the summer months (Umoh et al. 1995; Mathieu and deYoung 1995). Averaged throughout the year, however, in the Newfoundland Shelf region the atmosphere supplies more heat to the ocean than it extracts, of the order of 54 – 68 W/m^2. Umoh et al. (1995) also indicated that variations in the air–sea heat fluxes can account for up to 89% of the variance in the annual water temperature cycle on the Newfoundland Shelf.

During the period 1950–1989 the total heat transport H (baroclinic and barotropic) through the Bonavista section was calculated to be 9.4×10^{13} W compared with 7.0×10^{13} W during the period 1990–1993. This corresponds to a 26% reduction during the early 1990s, which is consistent with a decrease in the heat content of the water column at Station 27 during the same period (Fig. 5*b*) and also with the meteorological and ice anomalies experienced over the Northwest Atlantic during the early 1990s (Fig. 4). When

© 1997 NRC Canada

there is a net positive heat flux over the year into the ocean, then this heat has to be advected away by the local currents; otherwise the water temperature would rise. Therefore the heat flow through a cross section of the current gives some indication of the total heat flux Q from the atmosphere to the ocean over the upstream ocean surface area, since this heat is transported southward (in this area) by the currents throughout the year. The reduction in heat transport calculated here is of the same order as the low-frequency interannual variations in the total atmospheric heat flux shown by Umoh et al. (1995). This analysis suggests that much of the observed interannual variations in the ocean temperature may be explained by variations in the air–sea flux over the upstream area.

Summary

In spite of global warming trends the Northwest Atlantic has experienced below-normal air temperatures since the late 1980s. The deeper than normal low pressure system over Iceland during the winter months resulted in a stronger atmospheric circulation from the northwest bringing cold arctic air over eastern Canada and much of the Northwest Atlantic. The below-normal winter air temperatures resulted in increased ice production in northern areas and increased ice transport to lower latitudes and brought a colder and fresher water mass to the continental shelf during the spring and summer months. These anomalies reached a peak during the spring and early summer of 1991 when upper layer water temperatures fell to a record 3.0°C below normal and ice extent and duration were among the greatest and longest on record along the Newfoundland coast. Bottom temperatures over much of the continental shelf have been 0.5–1.0°C below normal since 1986, about 8 yr, the longest continuous period since measurements began in 1946.

The mean circulation determined from current measurements made during the period 1990–1993 using fixed current meters, drifting buoys, ADCPs, and calculations from density measurements compared well with previous estimates. The geostrophic transport through a transect across Hamilton Bank and off Cape Bonavista for the 1990s indicated no significant difference from that calculated from the 1950–1989 average. The current measurements made from fixed moorings along the Bonavista transect were in good agreement with the current field determined from the average of about 40 ADCP transects, except in the nearshore region where the current fluctuations were often larger than the mean flow. The total current field determined by referencing the geostrophic calculations to the ADCP measurements at 300 m depth appeared to be quite realistic; a total transport of about 11.9 Sv through the Bonavista line using these velocities was consistent with the earlier estimate of 11.0 Sv by Lazier and Wright (1993) through the Seal Island transect based on data from 1978 to 1987. Although the average transport during the early 1990s period was not significantly different from the long-term average, the differences in the temperature field alone effected a 26% reduction in the advective heat flux on the Newfoundland Shelf. These findings are consistent with the large-scale meteorological and ice anomalies experienced over the Northwest Atlantic during the early 1990s.

Acknowledgments

This work was supported through the Government of Canada's Atlantic Fisheries Adjustment Program (Northern Cod Science Program, NCSP) and the Ocean Production Enhancement Network (OPEN). We thank the many scientists who have contributed to the national data base (MEDS) over the years and the technical and computer staff at Northwest Atlantic Fisheries Centre for the professional quality of data acquisition and processing. We thank G. Mertz for reviewing this manuscript and for many useful discussions. We also thank two anonymous reviewers for many helpful comments and suggestions.

References

Akenhead, S. 1987. Temperature and salinity off Newfoundland: Station 27 annual cycle and residuals. NAFO SCR Doc. 87/66.

Bryan, K. 1962. Measurements of meridional heat transport by ocean currents. J. Geophys. Res. **67**: 3403–3414.

Chapman, D.C., and Beardsley, R.C. 1989. On the origin of shelf water in the Middle Atlantic Bight. J. Phys. Oceanogr. **19**: 384–391.

Colbourne, E.B. 1993*a*. Environmental conditions in Atlantic Canada, midsummer with comparisons to the long-term mean. NAFO SCR Doc. 93/106. Ser. No. N2299.

Colbourne, E.B. 1993*b*. Oceanographic conditions during the Annual Groundfish Survey in NAFO Divisions 2J3KL. NAFO SCR Doc. 93/88. Ser. No. N2273.

Colbourne, E.B., and Foote, K.D. 1994. Spatial temperature and salinity fields over the shelves of Newfoundland and Labrador. Can. Tech. Rep. Hydrogr. Ocean Sci. 160.

Colbourne, E.B., and Senciall, D. 1993. Temperature, salinity and sigma-*t* along the standard Bonavista transect. Can. Tech. Rep. Hydrogr. Ocean Sci. 150.

Colbourne, E.B., Helbig, J., and Cumming, D. 1993. Improved ADCP performance using a hydrodynamically designed boom mount. J. Atmos. Oceanic Technol. **10**(4): 629–636.

Colbourne, E.B., Narayanan, S., and Prinsenberg, S. 1994. Climate changes and environmental conditions in the Northwest Atlantic, 1970–1993. ICES Mar. Sci. Symp., **198**: 311–322.

Colbourne, E.B., Senciall D., and Foote, K.D. 1995. Temperature, salinity and sigma-*t* along the standard Seal Island transect. Can. Tech. Rep. Hydrogr. Ocean Sci. 164.

deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. **50**: 2729–2741.

deYoung, B., Perry F., and Greatbatch, R., 1994. Objective analysis of hydrographic data in the Northwest Atlantic. Can. Data Rep. Hydrogr. Ocean Sci. No. 130.

Drinkwater, K.F. 1993. Overview of environmental conditions in the Northwest Atlantic in 1992. Dep. Fish. Oceans, Atl. Fish. Res. Doc. 93/45.

Drinkwater, K.F., Petrie B., and Narayanan, S. 1992. Overview of environmental conditions in the Northwest Atlantic in 1991. NAFO SCR Doc. 92/73.

Findlay, B.F., and Deptuch-Stapf, A. 1991. Colder than normal temperatures over northeastern Canada during the 1980s. Clim. Perspect. Apr. Mon. Review, **13**: 9–12.

Fissel, D.B., and Lemon, D.D. 1991. Analysis of physical oceanographic data from the Labrador Shelf, summer 1980. Can. Contractor Rep. Hydrogr Ocean Sci. No. 39.

Gill, A.E. 1982. Atmosphere–ocean dynamics. Academic Press, New York.

Godin, G. 1972. The analysis of tides. University of Toronto Press, Toronto, Ont.

© 1997 NRC Canada

Greenberg, D.A., and Petrie, B.D. 1988. The mean barotropic circulation on the Newfoundland shelf and slope. J. Geophys. Res. **93**: 15541–15550.

Hachey, H.B., Hermann, F., and Bailey, W.B. 1954. The waters of the ICNAF Convention Area. Int. Comm. Northwest Atl. Fish. Annu. Proc. **4**: 67–102.

Helbig, J., Mertz, G., and Pepin, P. 1992. Environmental influences on the recruitment of Newfoundland/Labrador cod. Fish. Oceanogr. **1**(1): 39–56.

Jones, P.D., and Wigley, T.M.L. 1990. Global warming trends. Sci. Am. (Aug.). pp. 84–91.

Lazier, J.R.N., and Wright, D.G. 1993. Annual velocity variations in the Labrador Current. J. Phys. Oceanogr. **23**: 659–678.

Leetmaa, A. and Bunker, A.F. 1978. Updated charts of the mean annual wind stress, convergences in the Ekman layers, and Sverdrup transports in the North Atlantic. J. Mar. Res., **36**: 311–322.

Mathieu, T., and deYoung, B. 1995. Application of a mixed layer model to the inner Newfoundland Shelf. J. Geophys. Res. **100**: 21–936.

Mertz, G., Narayanan, S., and Helbig, J. 1993. The freshwater transport of the Labrador Current. Atmos.-Ocean **31**: 281–295.

Millero, F.J., Perron, G., and Desnoyers, J.E. 1973. Heat capacity of seawater solutions from 5 to 35°C and 0.5 to 22% chlorinity. J. Geophys. Res. **78**: 4499–4507.

Myers, A., Helbig, J. and Holland, D. 1989. Seasonal and interannual variability of the Labrador Current and West Greenland Current. ICES C.M. 1989/C:16.

Myers, R.A., Akenhead, S.A., and Drinkwater, K. 1990. The influence of Hudson Bay runoff and ice-melt on the salinity of the inner Newfoundland Shelf. Atmos.-Ocean, **28**: 120–157.

Myers, R.A., Drinkwater, K.F., Barrowman, N.J., and Baird, J.W. 1993. Salinity and recruitment of Atlantic cod (*Gadus morhua*) in the Newfoundland region. Can. J. Fish. Aquat. Sci. **50**: 1599–1609.

Narayanan, S. 1994. Current meter observations from Hamilton Bank and NE Newfoundland Shelf, 1990 to 1993. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 157.

Narayanan, S., Colbourne, E.B., and Fitzpatrick, C. 1991. Frontal oscillations on the NE Newfoundland Shelf. Atmos.-Ocean, **29**: 547–562.

Narayanan, S., Prinsenberg, S., and Colbourne, E.B. 1992. Overview of environmental conditions in 2J3KL NAFO subareas in 1991. NAFO SCR Doc. 92/6. Ser. No. N2039.

Narayanan, S., Carscadden, J., Dempson, J.B., O'Connell, M.F., Prinsenberg, S., Reddin, D.G., and Shackell, N. 1995. Marine climate off Newfoundland and its influence on Atlantic salmon (*Salmo salar*) and caplin (*Mallotus villosus*). *In* Climate change and northern fish populations. *Edited by* R.J. Beamish. Can. Spec. Publ. Fish. Aquat. Sci. **121**: 461–474.

Narayanan, S., Prinsenberg, S., and Smith, P.C. 1996. Current meter observations from the Labrador and Newfoundland shelves and comparisons with barotropic model predictions and IIP surface currents. Atmos.-Ocean, **34**(1): 227–255.

Peterson, I. 1987. A snapshot of the Labrador Current inferred from ice-flow movement in NOAA satellite imagery. Atmos.-Ocean, **25**: 402–415.

Petrie, B., and Anderson, C. 1983. Circulation on the Newfoundland Shelf. Atmos.-Ocean, **21**: 207–226.

Petrie, B., and Drinkwater, K. 1993. Temperature and salinity variability on the Scotian Shelf and in the Gulf of Maine 1945–1990. J. Geophys. Res. 98(No. C11): 20079–20089.

Petrie, B., Akenhead, S., Lazier J., and Loder, J. 1988. The cold intermediate layer on the Labrador and Northeast Newfoundland shelves, 1978–1986. NAFO Sci. Counc. Stud. **12**: 57–69.

Petrie, B., Loder, J., Lazier, J., and Akenhead, S. 1992. Temperature and salinity variability on the eastern Newfoundland shelf: the residual field. Atmos.-Ocean, **30**: 120–157.

Prinsenberg, S.J., Peterson, I.K., Narayanan, S., and Umoh, J.U. 1997. Interaction between atmosphere, ice cover, and ocean off Labrador and Newfoundland from 1962 to 1992. Can J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Rogers, J.C. 1984. The association between the North Atlantic oscillation and the southern Oscillation in the Northern Hemisphere. Mon. Weather Rev. **112**: 1999–2105.

Saulesleja, A. 1994. Summer review. Clim. Perspect. **16**.

Smith, E.H., Soule, F.M., and Mosby, O. 1937. The Marion and General Green expeditions to Davis Strait and Labrador Sea. Bull. U.S. Coast Guard No. 19.

Smith, P.C. 1983. The mean and seasonal circulation off southwestern Nova Scotia. J. Phys. Oceanogr. **13**: 1034–1054.

Templeman, W. 1975. Comparison of temperature in July–August hydrographic sections of the eastern Newfoundland area in 1972 and 1973 with those from 1951 to 1971. ICNAF Spec. Publ. **10**: 17–39.

Umoh, J.U., Loder, J.W., and Petrie, B. 1995. The role of air–sea heat fluxes in annual and interannual ocean temperature variability on the eastern Newfoundland Shelf. Atmos.-Ocean, **33**: 531–568.

© 1997 NRC Canada

Relating oxygen levels in the Newfoundland offshore waters to the physiology of Atlantic cod (*Gadus morhua*)

J.W. Kiceniuk and E. Colbourne

Abstract: During the Northern Cod Science Program (NCSP), dissolved oxygen was measured routinely on oceanographic surveys on the Newfoundland Shelf from 1992 to 1994. A periodic regression was fitted to historical oxygen data to obtain a seasonal mean oxygen content, and divergences (anomalies) from the mean were examined. Anomalies were negative (below the photic zone) in the mid-1930s and 1960s and were lower in the early 1980s when data collection stopped until 1992. When data collection resumed in 1992 the anomalies were the lowest of the whole time series. Positive anomalies were found in the 1950s, early 1970s, and in 1993. Mean percent saturation values (% sO_2) were also calculated for the Bonavista transect. In the historical mean for the Bonavista transect the minimum was 80% saturation. This minimum covered about 60% of the shelf from the shore outward. The levels of % sO_2 for June, July, and September of 1992 were lower than the historical mean by about 10% sO_2. In 1993 the levels were slightly higher than the mean. The lowest % sO_2 found on the shelf in 1992 (65% sO_2) is close to the published incipient lethal level of 60% sO_2.

Résumé : Dans le cadre du Programme de recherche scientifique sur la morue du Nord, l'oxygène dissous était mesuré systématiquement au cours des études océanographiques qui ont été réalisées sur la plate-forme de Terre-Neuve de 1992 à 1994. Nous avons appliqué une régression périodique aux données chronologiques portant sur l'oxygène afin d'obtenir une moyenne saisonnière de la teneur en oxygène; les écarts par rapport à cette moyenne (anomalies) ont été étudiés. Les anomalies étaient négatives (au-dessous de la zone euphotique) au milieu des années 30 et dans les années 60, et elles étaient moindres au début des années 80 lorsque la saisie des données a été interrompue jusqu'en 1992. Quand cette dernière a repris en 1992, les anomalies étaient les moins importantes enregistrées sur l'ensemble de la période. Nous avons noté des anomalies positives pour les années 60, pour le début des années 70 et pour l'année 1993. Les valeurs moyennes de saturation (% sO_2) ont également été calculées pour la section de Bonavista. Dans le cas de la moyenne historique correspondant à cette section, la valeur minimale de saturation était de 80 %. Ce minimum s'appliquait à environ 60 % de la plate-forme, de la côte vers le large. Les niveaux de % sO_2 pour les mois de juin, juillet et septembre 1992 étaient inférieurs d'environ 10 % sO_2 à la moyenne historique. En 1993, les niveaux étaient un peu plus élevés que la moyenne. La valeur de % sO_2 la plus basse enregistrée sur la plate-forme en 1992 (65 % sO_2) était proche de la valeur de 60 % sO_2 qui est présentée dans les publications comme étant le niveau auquel des effets mortels commencent à se faire sentir.
[Traduit par la Rédaction]

Introduction

Oxygen exchange in fish

Oxygen is a critical prerequisite for life of most fish. Exchange of oxygen across respiratory organs of organisms occurs by the physical process of diffusion of the gas across the epithelium and into the blood or tissue. A net diffusion of gas occurs only in the presence of a partial pressure gradient of the gas. When a gas dissolves in water, its concentration (at a given temperature and salinity) is proportional to its partial pressure. Partial pressure (pO_2) as the term implies, is the proportion of total pressure that is attributable to the gas in question. The partial pressure of a gas in water at equilibrium with the atmosphere is equal to its partial pressure in air of 100% relative humidity. Partial pressure is neither temperature nor salinity dependent.

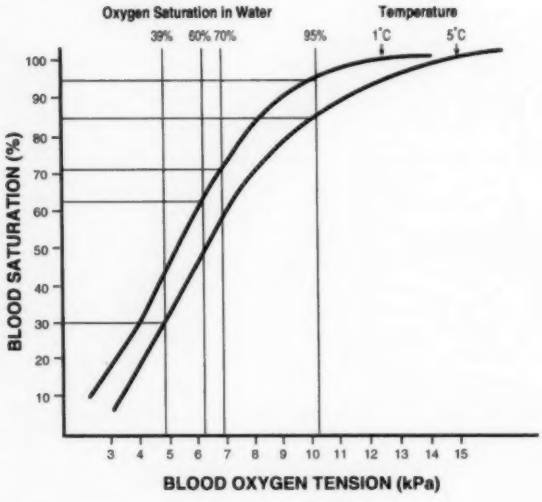
Historically, oxygen was measured as the chemical quantity by titration, and titration is still used for the quality control of oxygen determinations by electronic means. Although oxygen sensors that are now in common usage on high-speed oceanographic profiling instruments measure pO_2 the pO_2 values are secondarily converted to oxygen content. Percent saturation (% sO_2) is the ratio of the concentration of oxygen in water to the concentration of oxygen in water saturated with air. Conceptually, % sO_2 is similar to pO_2 except that the former does not take into account the vapour pressure of water, which is very small at temperatures <5.0°C (≈1 kPa at 5.0°C). Partial pressure and percent saturation are measures of the physical availability of a gas whereas oxygen content is a measure of the chemical quantity of oxygen. Although oxygen content of the water column is important oceanographically as a tracer of water masses, it has few physiological consequences for marine organisms. The biologically relevant oxygen variables are "percent saturation" and "partial pressure," since these are what determine oxygen uptake from the surrounding water and blood saturation levels in

Received February 22, 1995. Accepted February 8, 1996.
J13441

J.W. Kiceniuk and E. Colbourne. Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

© 1997 NRC Canada

Fig. 1. Relationship of cod blood oxygen saturation to blood oxygen tension. Environmental oxygen saturation levels corresponding to blood oxygen tensions are also given. (From Karpov and Novikov 1980; Claireaux and Dutil 1992).



organisms. Percent saturation (% sO_2) is given by the relationship

$$\% \, sO_2 = C/C_{sat} \cdot 100$$

where C is the in situ measured oxygen concentration and C_{sat} is the concentration of oxygen in water saturated with air. The solubility of oxygen (C_{sat}) in seawater is determined by least-squares fits to experimental data at various temperatures and salinities and is given in Weiss (1970).

The large temperature effect on oxygen solubility in water makes the interpretation of oxygen content, in the context of biological systems, impossible unless the effect of temperature is eliminated. In the deep waters of the Northwest Atlantic the temperature variation is so restricted as to have a rather small effect on oxygen solubility; it is therefore valid to compare oxygen content values in these confines, but it is not valid to generalize to other conditions. For example, oxygen saturation values of seawater decrease from about 8.0 mL/L at 0.0°C to about 5.0 mL/L at 20.0°C at a salinity of 34.0 psu. The effect of salt is insignificant; for example, at a constant temperature of 0.0°C, saturation values decrease from 8.3 mL/L at a salinity of 30.0 psu to 8.1 mL/L at a salinity of 35.0 psu (Weiss 1970).

Oxygen requirements of cod

Both pO_2 and % sO_2 can be related to the respiratory requirements of fish. In the case of Atlantic cod (*Gadus morhua*) in oxygen-saturated water (pO_2 = 21 kPa) the pO_2 in blood is about 10 kPa. When cod are exposed to a pO_2 of 8.0–9.0 kPa (≈39% saturation), they accumulate lactate and pyruvate in the muscle and heart (Claireaux and Dutil 1992). The accumulation of these end-products of glycolysis is indicative of insufficient oxygen supply to the tissues (anaerobiosis). The reason for this anaerobiosis is evident in Fig. 1, where the arterial pO_2 values from Claireaux and Dutil (1992) have been combined with the blood oxygen saturation data of Karpov and Novikov (1980). At a seawater saturation level of 39%, at 5.0°C, the arterial blood saturation of cod is only about 30% saturated. At a water saturation of 70% sO_2, cod are only able to saturate their blood to 70% at 1.0°C and to about 55% at 5.0°C. At ≈60% sO_2, cod respire about three times as much water as at normoxia (Saunders 1963), and therefore have reduced aerobic scope. The low aerobic scope plus the additional energy demand for maintenance (ventilatory and cardiac pumping) are reflected in the incipient lethal level of oxygen for cod which has been reported as 60% sO_2 (Scholz and Waller 1992). It has also been shown that cod infected with *Lernaeocera branchialis* are more susceptible to low oxygen levels (Scholz and Waller 1992). The effects of trypanosome infection should be similar, since this parasite depletes the hemoglobin levels of host cod (Khan 1977). Both parasites are common in Atlantic cod in Newfoundland waters, and the cod in NAFO Divisions 2J and 3K have very high infection rates (Khan et al. 1980). It is not known what the incipient lethal oxygen saturation levels are for cod harbouring these parasites.

Low oxygen levels have been observed in many coastal locations in the North Sea in the early 1980s (Dethlefsen and Westernhagen 1983; Dethlefsen 1987) and since the early 1980s in the Baltic Sea (Weigelt and Rumohr 1986; Gerlach 1988; Kils et al. 1989; Weigelt 1990). Recent work in the Gulf of St. Lawrence (D'Amours 1993) has shown that the distribution of cod is sensitive to hypoxia and that cod completely avoid regions of oxygen levels below a threshold of 3.4 mg/L, but it is not possible from the published report to determine the corresponding pO_2 or sO_2. A paper on the effects of low oxygen (hypoxia) on cod in the German Bight indicates that cod begin to die at oxygen saturation levels of 60% (Scholz and Waller 1992). Other studies have indicated that the normal metabolic rate of cod decreases at low oxygen levels (Sundnes 1957; Saunders 1963). Recent laboratory experiments have also indicated that oxygen saturation levels below 75% may inhibit the proper development of cod eggs (J. Anderson, DFO, St. John's, Nfld., personal communication).

We have reviewed the biophysical aspects of oxygen exchange in marine organisms and the physiological implications to fish exposed to environmental hypoxia. We now use historical and recently collected dissolved oxygen data to examine the possible occurrence of oxygen levels on the Newfoundland Shelf that may be detrimental to cod.

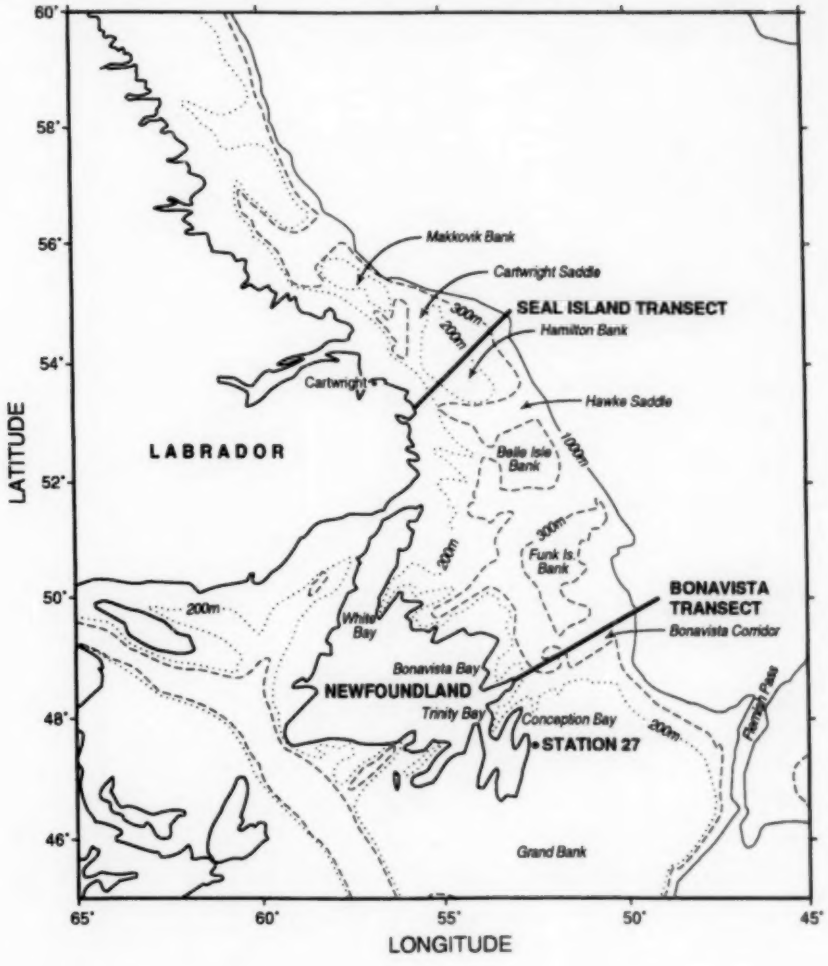
Materials and methods

Dissolved oxygen data were routinely collected along transects off the east coast of Newfoundland (Fig. 2) on oceanographic research surveys in June, July, and September of 1992 and 1993. The measurements were made with Beckman and YSI type polarographic element dissolved oxygen sensors with factory calibrated endpoints at 0 and 100% saturated water oxygen levels. The sensors were interfaced to pumped Seabird-911 and SBE-25 conductivity–temperature–depth (CTD) systems which simultaneously measured conductivity, temperature, and depth.

Field calibrations of the oxygen sensors were carried out by taking water samples with Niskin bottles triggered at standard depths during the CTD upcast. The average sensor oxygen values collected

© 1997 NRC Canada

Fig. 2. Location map of the study area showing the position of the standard transects.



during each stop were compared with the titrated values. The oxygen contents of the samples were determined by semiautomated analytical chemistry using a modified Winkler titration technique where the endpoint was detected photometrically (Jones et al. 1992). Typically, about 250 water samples were titrated in duplicate on each survey for quality control of the electronic measurements.

On the oceanographic surveys during 1992 and 1993, measurements were made at station separations of about 15 km along transects running from the inshore areas along the east coast of Newfoundland and offshore to the edge of the continental shelf. The vertical profiles of oxygen concentration were quality controlled and linearly interpolated to 5.0-m depth intervals. The measured oxygen concentrations (millilitres per litre) are converted to % sO_2 by dividing the measured oxygen concentration by the computed solubility of oxygen in seawater at the measured temperature and salinity as discussed above. Vertical cross sections of % sO_2 were contoured along the Cape Bonavista transect (Fig. 2) for each survey.

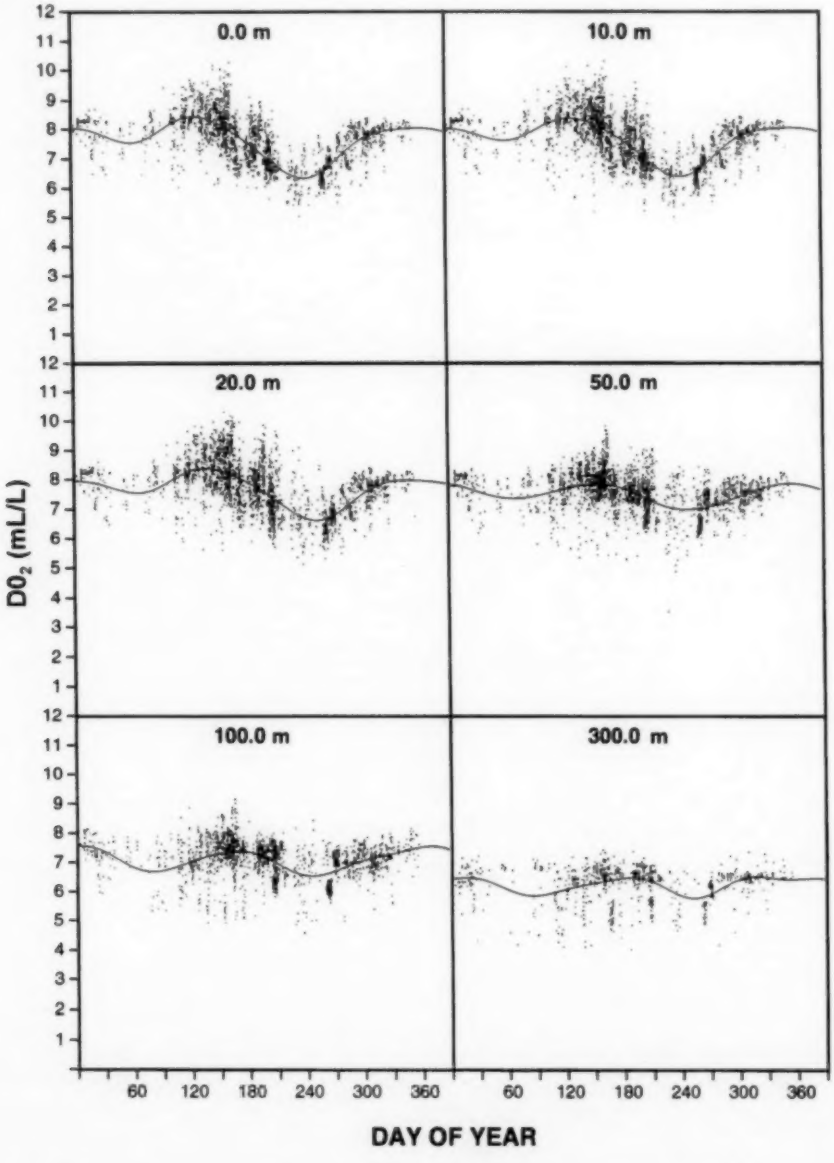
All available historical oxygen data on the Newfoundland Shelf from the Grand Bank to Hamilton Bank were retrieved from archives at the Marine Environmental Data Service (MEDS), Ottawa, Ont., and sorted by day of the year and the seasonal cycle determined by fitting a least-squares regression of the form $\cos(\omega t - \phi)$ to the annual mean and a sum of four harmonics at frequencies ω and phase ϕ at selected water depths. Time series of dissolved oxygen concentration and anomalies were then formed by taking each available observation and subtracting the amplitude of the least-squares fitted value of the seasonal cycle for the same day of the year. In addition the historical data on the Newfoundland Shelf from the Grand Banks in the south to Hamilton Bank in the north were used to construct an average cross-shelf vertical transect of oxygen saturations for the month of July.

Results and discussion

Variations between the duplicate titrations for the determination of oxygen content were between 0.005 and 0.03 mL/L. Typical least-squares linear regressions of the titration measurements (for a trip of 8–10 d) to the electronic sensor measurements had slopes near 1.0 and intercepts between 0.1 and 0.2, with r^2 around 0.8. The calibration results usually showed the sensor reading somewhat lower than the titrated

© 1997 NRC Canada

Fig. 3. Dissolved oxygen values on the Newfoundland Shelf for all available years at various depths, together with the fitted regression curves to the seasonal cycles.



values. However, the offset was always near linear, as indicated by the slope of the fitted equation across the range of oxygen concentrations encountered on the Newfoundland Shelf (about 6.0–8.0 mL/L).

The historical oxygen data at the selected water depths together with the fitted seasonal cycle show, as one would expect, that the largest seasonal cycle occurs in the upper layers, with the amplitude decreasing with depth until it is not significant below 200 m depth (Fig. 3). The oxygen levels generally increase during the winter months due to strong vertical mixing from storm activity. During the spring the oxygen levels reach their maximum levels in early May in the surface layers and late June in deeper water, corresponding to the annual phytoplankton bloom. During the summer months the levels decrease, corresponding to reduced mixing of the water column and increased consumption by zooplankton. A weak maximum occurs during the fall period, corresponding to a weaker secondary plankton bloom.

The time series of oxygen anomalies at various depths from the surface to 400 m depth at the edge of the continental shelf showed that in general oxygen values increased slightly from below-average conditions during the early 1950s to near-average values during the 1960s, corresponding to warming oceanographic conditions (Fig. 4). During the early

© 1997 NRC Canada

Fig. 4. Time series of dissolved oxygen anomalies referenced to the long-term average at standard depths.

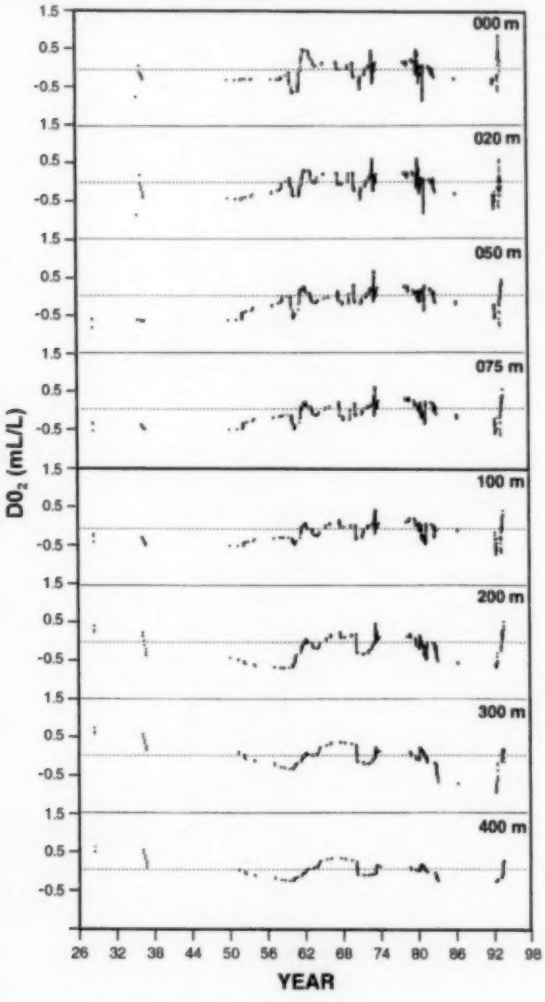
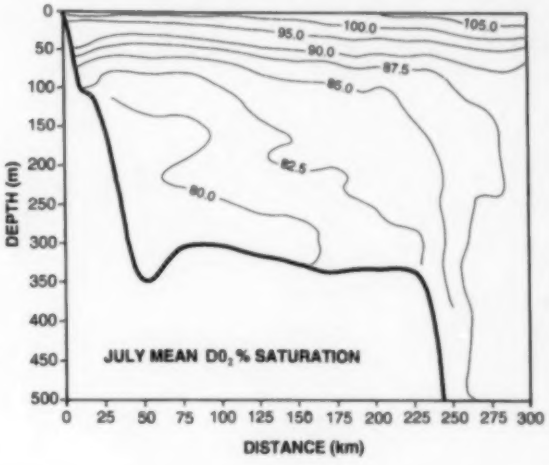


Fig. 5. Average July dissolved oxygen saturation cross section for the Bonavista transect, based on all available data.



to mid-1980s and again in 1992 the anomalies were again below average, corresponding to cold conditions (Colbourne et al. 1994). The anomaly at 300 m depth, near bottom over most of the northeast Newfoundland Shelf, was lower in 1983 than at any other previous time within the period of the data set. Very few data were available from 1984 to 1991 when the northern cod stocks experienced large declines. When data became available in 1992, anomalies were the lowest ever observed at depth on the Northeast Newfoundland Shelf. Data from 1993, however, indicated a return to above-average conditions.

In the July transect, average oxygen saturations ranged from 100% in the surface layers to 90% at 50 m depth and from 80% near bottom at midshelf to 85% at the shelf break. (Fig. 5). At middepth over the shelf in the core of the cold intermediate layer (CIL) (Petrie et al. 1988), values generally ranged from 80 to 85% saturation. Beyond the shelf break, in the North Atlantic water, oxygen saturations were generally above 87%.

In the oxygen saturation profiles along the Bonavista transect for June, July, and September of 1992 and 1993 the values ranged from about 80 to 100% from the surface to about 50 m depth (Fig. 6) as a result of mixing of the surface layer by wave action and the patchy distribution of biological activity. In the depth range from 50 to 250 m from the inshore areas to approximately midshelf about 150 km offshore the oxygen saturation was about 75–80% in 1992 and generally around 85–90% in 1993. This area roughly corresponds to the CIL and the Labrador current.

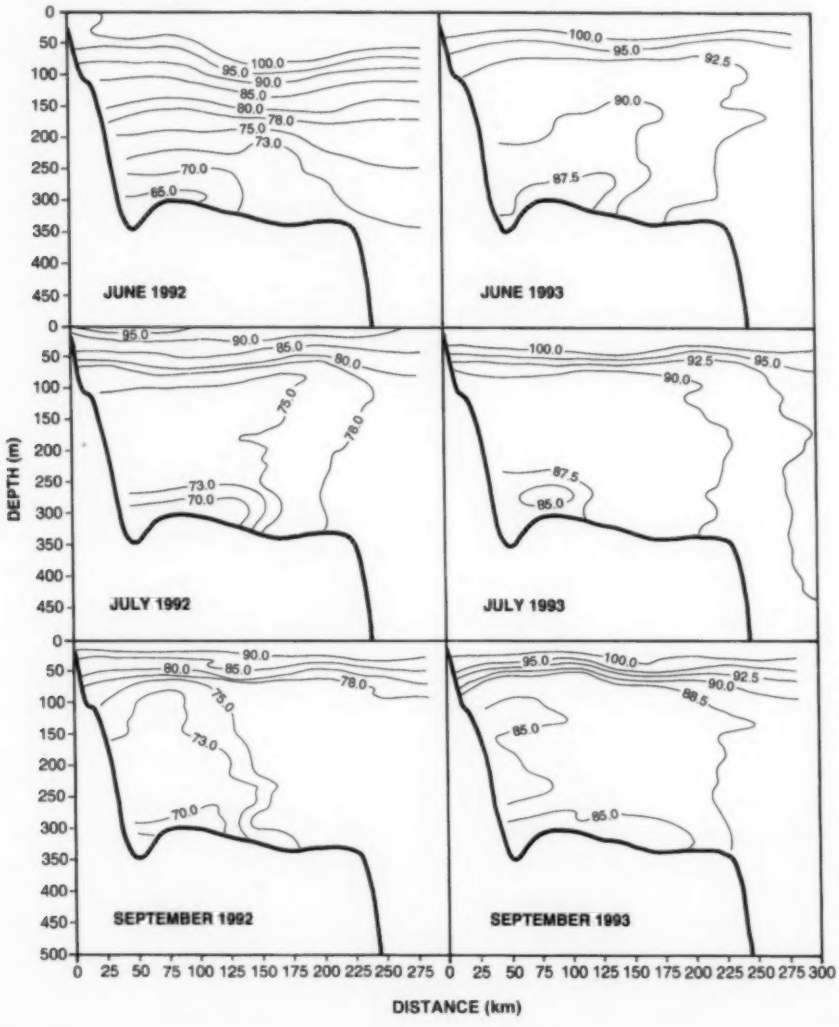
Near the bottom, saturations were about 90% in water depths from 0 to about 100 m and 65–70% in water depths from 250 to 350 m. Further offshore outside the CIL near the shelf edge, saturations generally ranged from 75 to 80%, with some areas as low as 65–70% in 1992 and from 85 to 90% in 1993. Oxygen saturation levels as low as 65% were reported in the 1960s on the Grand Banks southeast of Newfoundland (Ponomarenko and Istoshino 1963). It is noteworthy that cod concentrations were found in the waters at the shelf edge where we found the highest bottom % sO_2 levels. In general the 1993 oxygen saturation values were up to 10% higher than the 1992 values with no evidence of oxygen-depleted water on the continental shelf off Newfoundland and Labrador.

The low % sO_2 levels found during 1992 close to the bottom on the shelf are stressful and energetically costly to cod (Saunders 1963; Scholz and Waller 1992). However, until the preference levels of oxygen are available for all life stages of cod the relative importance of recent oxygen levels in the Newfoundland waters remains unknown.

The historical oxygen data base has significant gaps, particularly during the 1980s, and most data that are available are from specific transects. No oxygen data were collected during the groundfish surveys from 1978 to 1993, and it is therefore difficult to relate oxygen levels directly to cod distributions and recruitment during that period. There is a need for % sO_2 data from a larger area, particularly in relation to the three-dimensional distribution of cod.

© 1997 NRC Canada

Fig. 6. June, July, and September dissolved oxygen saturation cross sections for the Bonavista transect for 1992 and 1993.



Acknowledgments

This work was supported through the Government of Canada's Atlantic Fisheries Adjustment Program (NCSP). We thank J. Morgan and W.R. Bowering and two anonymous reviewers for helpful comments and suggestions. We thank C. Fitzpatrick, D. Senciall, P. Stead, and J. Walpert of the Northwest Atlantic Fisheries Centre for the professional quality of data collection and calibration. We also thank D. Foote for help with the data analysis.

References

Claireaux, S., and Dutil, J.D. 1992. Physiological response of the Atlantic cod (*Gadus morhua*) to hypoxia at various environmental salinites. J. Exp. Biol. **163**: 97–118.

Colbourne, E.B., Narayanan, S., and Prinsenberg, S. 1994. Climatic changes and environmental conditions in the Northwest Atlantic, 1970-1993. ICES Mar. Sci. Symp. **198**: 311–322.

D'Amours, D. 1993. The distribution of cod (*Gadus morhua*) in relation to temperature and oxygen level in the Gulf of St. Lawrence. Fish. Oceanogr. **2**: 24–29.

Dethlefsen, V. 1987. Sauerstoffmangel und Krankheiten der Kliesche (*Limanda limanda*) in der ostlichen Nordsee. Inf. Fischwirtsch. **34**(4): 166–170.

Dethlefsen, V.V., and von Westernhagen, H. 1983. Oxygen deficiency and effects on bottom fauna in the eastern German Bight 1982. Meeresforschung, **30**: 42–53.

Gerlach, S.A. 1988. The Baltic environment. Proceedings of the 10th Symposium of the Baltic Marine Biologists. Sonderheft Kieler Meeresforschungen, **6**.

Jones, E.P., Zemlyak, F., and Stewart, P. 1992. Operating manual for the Bedford Institute of Oceanography automated dissolved oxygen titration system. Can. Tech. Rep. Hydrogr. Ocean Sci. 138.

Karpov, A.K., and Novikov, G.G. 1980. Hemoglobin alloforms in cod, *Gadus morhua* (Gadiformes, Gadidae), their functional characteristics and occurrence in populations. J. Ichthyol. **20**: 45–49.

Khan, R.A. 1977. Blood changes in Atlantic cod (*Gadus morhua*)

© 1997 NRC Canada

infected with *Trypanosoma murmanensis*. J. Fish. Res. Board Can. **34**: 2193–2196.

Khan, R.A., Murphy, J., and Taylor, D. 1980. Prevalence of a trypanosome in Atlantic cod (*Gadus morhua*) especially in relation to stocks in the Newfoundland area. Can. J. Fish. Aquat. Sci. **37**: 1467–1475.

Kils, U., Waller, U., and Fischer, P. 1989. The fish kill of autumn 1988 in Kiel Bay. ICES C.M. L:14.

Petrie, B., Akenhead, S., Lazier, J., and Loder, J. 1988. The cold intermediate layer on the Labrador and Northeast Newfoundland shelves, 1978–1986. NAFO Sci. Counc. Stud. **12**: 57–69.

Ponomarenko, L.S., and Istoshino, M.A. 1963. Hydrochemical studies in the Newfoundland area. *In* Soviet fisheries investigations in the Northwest Atlantic. Edited by Y.Y. Marti. Israel Program for Scientific Translations, Jerusalem. pp. 113–124.

Saunders, R.L. 1963. Respiration of the Atlantic cod. J. Fish. Res. Board Can. **20**: 373–386.

Scholz, U., and Waller, U. 1992. The oxygen requirements of three fish species from the German Bight: cod *Gadus morhua*, plaice *Pleuronectes platessa*, and dab *Limanda limanda*. J. Appl. Ichthyol. **8**: 72–76.

Sundnes, G. 1957. On the transport of live cod and coalfish. J. Cons. Cons. Int. Explor. Mer, **22**: 191–196.

Weigelt, M. 1990. Oxygen conditions in the deep water of Kiel Bay and the impact of inflowing salt-rich water from the Kattegat. Meeresforschung Rep. Mar. Res. **33**: 1–22.

Weigelt, M., and Rumohr, H. 1986. Effects of wide-range oxygen depletion on benthic fauna and demersal fish in Kiel Bay 1981–1983. Meeresforschung Rep. Mar. Res. **31**: 124–136.

Weiss, R.F. 1970. The solubility of nitrogen, oxygen and argon in water and seawater. Deep-Sea Res. **17**: 721–735.

© 1997 NRC Canada

Influence of plasma antifreeze glycoproteins on temperature selection by Atlantic cod (*Gadus morhua*) in a thermal gradient

S.V. Goddard, M.J. Morgan, and G.L. Fletcher

Abstract: Atlantic cod (*Gadus morhua*) produce antifreeze glycoproteins when exposed to cold conditions in winter which increase their physiological resistance to extreme low temperatures. Two size categories of cod (23–31 and 40–60 cm), containing subgroups with and without antifreeze, were acclimated to 2°C (November–February). A thermal gradient (–0.5 to 1°C approximately) was established in a compartmented trough and fish were introduced into the temperature gradient singly (experiments conducted between December and February). Frequency of occupation of the compartments and temperatures throughout the trough were recorded during hour-long observation periods. Mean gradient temperatures occupied by cod in the four groups (large and small, with and without antifreeze) were not correlated with plasma antifreeze levels. Cod with antifreeze did not show a preference for subzero water. Overall, large cod occupied a lower mean temperature than small cod. However, small cod with antifreeze occurred significantly more frequently in the cold and less in the warm and middle gradient areas than did small cod with no antifreeze. This effect was not seen in the two groups of large cod. Thus, the presence of plasma antifreeze increased the likelihood of small cod entering water at subzero temperatures, while having no such effect on large cod.

Résumé : Les morues franches (*Gadus morhua*) produisent des glycoprotéines antigel lorsqu'elles sont exposées au froid durant l'hiver, ce qui augmente leur résistance physiologique aux températures extrêmement basses. Des morues divisées en deux catégories de taille (23–31 cm et 40–60 cm), et subdivisées en groupes possédant ou non l'antigel, ont été acclimatées à une température de 2°C (novembre à février). Un gradient de température (de –0,5 à 1°C, approximativement) a été établi à l'intérieur d'une auge compartimentée; les poissons ont été exposés à ce gradient de température un par un (expériences réalisées de décembre à février). La fréquence d'occupation des différents compartiments, de même que les températures, ont été enregistrées à travers toute l'auge, au cours de périodes d'observation de 1 h. Les températures moyennes des compartiments occupés par les morues n'étaient pas en corrélation avec les concentrations d'antigel dans le plasma, et ce, pour les quatre groupes (grandes et petites morues, avec et sans antigel). Les morues possédant l'antigel n'ont pas manifesté de préférence pour les températures inférieures à zéro. Dans l'ensemble, les grandes morues ont occupé des compartiments dont la température moyenne était plus basse que celle des compartiments occupés par les petites morues. Cependant, les petites morues possédant l'antigel se retrouvaient, de façon significative, plus souvent dans les compartiments froids et moins souvent dans les parties chaudes ou moyennes du gradient que les petites morues dépourvues d'antigel. Cet effet n'a pas été observé dans les deux groupes de grandes morues. La présence d'antigel dans le plasma a donc augmenté la probabilité pour les petites morues de pénétrer dans de l'eau à des températures inférieures à zéro, alors qu'elle n'avait pas cet effet chez les grandes morues.
[Traduit par la Rédaction]

Introduction

Seawater temperatures below –1.0°C are common off the coast of Newfoundland and Labrador and, depending on salinity, temperatures can fall to –1.8°C before freezing occurs (Templeman and Fleming 1956; Narayanan et al. 1992; Fissel and Tang 1991). Atlantic cod (*Gadus morhua*) plasma normally freezes at temperatures around –0.7°C (Simpson 1953). Cod could thus reasonably be expected to avoid areas where they might experience cooling of their body fluids to levels below the freezing point, with the resultant danger of internal ice crystal formation and death (Fletcher et al. 1982). Generally, this appears to be so. Adult and late juvenile Atlantic cod (those that have reached the migratory phase of their life cycle) are most often found in water at temperatures above 0°C in the wild (Taggart and Frank 1987; Rose et al. 1994; Swain and Kramer 1995). However, there are reports of adult northern cod occupying subzero waters throughout their range, sometimes for short periods, for example, during inshore–offshore migrations through the cold intermediate layer (CIL), and sometimes for considerably longer (months) (Templeman and Fleming 1965; Lear et al. 1986; Petrie et al. 1988; Goddard et al. 1994; Rose et al. 1994; Wroblewski et al. 1994).

Juvenile northern cod are more commonly found in sub-

Received February 15, 1995. Accepted March 18, 1996.
J13443

S.V. Goddard and G.L. Fletcher. Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada.
M.J. Morgan. Department of Fisheries and Oceans, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

© 1997 NRC Canada

Table 1. Four experimental groups tested in a low-temperature gradient.

Group	Acclimation temp. (°C)	Photoperiod	Thermal hysteresis (°C)	Length (cm)	*n*
Large cod					
No AFGP	2.1 ± 0.1	24/0	0.07 ± 0.007	48.2 ± 5.0	11
AFGP	2.1 ± 0.1	24/0	0.24 ± 0.063	50.8 ± 5.6	10
Small cod					
No AFGP	2.2 ± 0.1	24/0	0.07 ± 0.01	26.8 ± 2.2	10
AFGP	2.1 ± 0.6	8/16	0.30 ± 0.104	27.2 ± 1.7	12

Notes: Values of length and thermal hysteresis (a measure of antifreeze glycoprotein (AFGP) activity) are given as means ± 1 SD for each experimental group. *n* = numbers of fish in each group. Acclimation temperature = mean temperature in each holding tank ± 1 SD throughout the course of the experiment. Photoperiod is presented as hours light/hours darkness.

zero water in winter, since they do not migrate but remain in the vicinity of their nursery grounds, the coastal regions of Newfoundland and Labrador or over the associated Banks (Lear and Green 1984; Rose et al. 1994; Taggart et al. 1994). Such waters are generally shallower and colder than those inhabited by the adults.

In common with many teleost species inhabiting areas where water temperatures fall below 0°C for all or part of the year, Atlantic cod can increase their freeze resistance by producing antifreeze glycoproteins. Exposure to temperatures of 0°C and below appears to be critical for development of high antifreeze levels in adults, while juveniles commence production earlier in the winter at higher environmental temperatures than the adults, and produce significantly greater quantities of antifreeze (Fletcher et al. 1987; Goddard et al. 1992, 1994).

Antifreeze molecules are found in the blood and extracellular fluids, where they lower the freezing point by approximately 200–300 times more than would be expected on the basis of colligative properties alone (DeVries 1988). In addition, they are believed to act at the cell membrane to increase cell tolerance to hypothermic temperatures (Rubinsky et al. 1992). In the wild, adult and juvenile northern cod have been found both inshore and offshore with antifreeze present in the plasma during the winter and spring months (Goddard et al. 1994; S.V. Goddard, unpublished observations).

The primary function of antifreeze in cod is to increase the cod's chances of living successfully at subzero temperatures. Since cod (particularly the adults) appear to require exposure to 0°C to accumulate high levels of antifreeze but require antifreeze to tolerate prolonged exposure to 0°C, we asked, "Do antifreeze glycoproteins modify behaviour so that cod with antifreeze in the plasma are more likely to enter bodies of cold water than those without?" This study was carried out to determine whether the presence of antifreeze proteins in the blood influenced the temperatures selected by adult and juvenile cod in a low-temperature thermal gradient.

Materials and methods

All the cod used in these experiments were caught in the coastal waters of eastern Newfoundland. Large (late juvenile/adult) and small (juvenile) cod were considered separately, as all previous work has shown that the physiology of antifreeze production is different between the two, reflecting their different overwintering strategies (Fletcher et al. 1987; Goddard et al. 1992; Goddard and Fletcher 1994).

Four experimental groups were established on October 28, 1992. Two of these groups were made up of large cod with a length range of 40–60 cm (overall mean length ± 1 SE = 49.5 ± 1.1 cm, $n = 21$). Northern cod in this length range can be considered late juvenile/adult (Taggart et al. 1994). The remaining two groups contained small (juvenile) cod with a length range of 23 – 31 cm (overall mean length ± 1 SE = 27.1 ± 0.4 cm, $n = 22$).

All the large cod were maintained in a 3000-L holding tank supplied with running aerated seawater at 2°C and were exposed to 24-h daylength (continuous illumination of the tank room). In general, adult cod require exposure to a temperature regime that declines to 0°C and below in order to accumulate high levels of antifreeze in the plasma (Fletcher et al. 1987; Goddard et al. 1994). However, we found that at 2°C, some of our large cod were producing antifreeze and that they had low to medium concentrations of antifreeze in their plasma. Others, maintained in the same holding tank, had no plasma antifreeze. Thus, prior to any trials in the thermal gradient, all the large cod were individually tagged for identification and were screened for the presence or absence of antifreeze proteins. Results of the screening allowed the later identification of the two experimental categories of large cod, with and without antifreeze (Table 1).

Photoperiod has no effect on the appearance of antifreeze in adult cod plasma (Fletcher et al. 1987). However, both temperature and photoperiod influence antifreeze production in juvenile Atlantic cod. While all juveniles appear to be able to accumulate plasma antifreeze at 2°C (Goddard et al. 1992), we have found that long daylength has an inhibitory effect on the production of antifreeze in such fish (S.V. Goddard, unpublished observations). Therefore, juvenile cod were kept in two separate 300 L tanks supplied with running, aerated seawater. Both tanks were kept at 2°C, but one group was exposed to 24 h of light, while the other was screened and exposed to the 8 h : 16 h light–dark cycle typical of a Newfoundland winter (Table 1). Temperatures in each holding tank were measured several times a week from October 28 and throughout the course of the experimental period (November 25, 1992 – February 12, 1993).

Temperature selection was tested in a 3 × 1.5 × 1.2 m high trough filled to a depth of 0.9 m with seawater. The long axis of the trough was divided into five compartments, each of which could be individually temperature controlled (for a full description, see Morgan 1993). Circular holes were cut in the partitions between the compartments to permit all fish to swim easily from one compartment to another. The temperature in each compartment was recorded at the beginning and end of each trial.

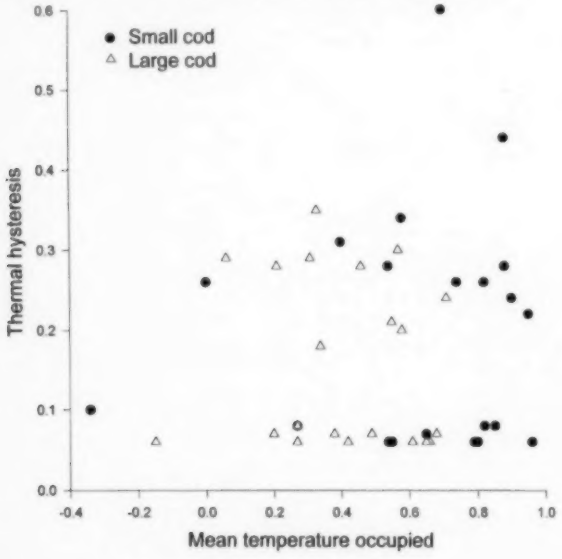
We were primarily interested in whether possession of anti-

© 1997 NRC Canada

Table 2. Overall mean temperatures in each of the five compartments of the gradient presented to the four experimental groups of cod.

Group	Mean gradient profile (°C)				
Large cod without antifreeze	0.88	0.56	0.18	–0.15	–0.29
Large cod with antifreeze	0.93	0.58	0.21	–0.12	–0.33
Small cod without antifreeze	0.93	0.54	0.14	–0.15	–0.30
Small cod with antifreeze	0.95	0.47	–0.01	–0.41	–0.66

Fig. 1. Thermal hysteresis (antifreeze) levels (°C) against mean temperatures occupied (°C) for all cod tested. All points at or below 0.08°C on the *y*-axis represent those fish with no plasma antifreeze, while those at 0.1°C or above represent fish with antifreeze.



freeze would modify behaviour with respect to temperatures of 0°C and below. Thus, gradients of short range with 0°C as the (ideal) midpoint were established. It was technically difficult to achieve identical gradients for each trial, since the trough was large and conditions in the tank room varied somewhat from day to day. However, for all trials, cod were presented with a gradient in which the midcompartment was approximately 0°C flanked by positive and negative temperatures (Table 2). Cod have been shown to be able to discern a temperature difference of 0.05°C (Bull 1936), and therefore, we assumed that this range would be sufficient to permit choice of thermal environment. The warm and cold ends of the gradient were reversed twice over the course of the experimental period to control for possible end effects of the trough. Each compartment was bubbled gently to provide aeration and maintain an approximately even internal temperature. Illumination was provided equally in all five compartments of the trough by using five 25-W lightbulbs, one bulb suspended over each compartment. Each cod was tested only once.

For each trial, one individual was placed in the trough and allowed to acclimate for 1 h prior to testing. The fish was then observed for 1 h and the compartment occupied was recorded at the start of the observation period and then at 2-min intervals thereafter, giving a total of 31 observations per fish. Only fish that made at least one transition between compartments during the acclimation period and/or trial were included in the analyses. Of the 43 fish examined, 41 explored the trough during the trial, while two fish explored during the acclimation period only and had settled in one compartment by the start of the observation period. After each trial, the fish was removed and a blood sample was taken.

All blood samples (1-cm^3) were taken from a caudal blood vessel using a 1 cm^3 syringe fitted with a 23- or 25-gauge needle. Sampling took less than 1 min and no anaesthetic was used. Blood was heparinized in Vacutainers containing sodium heparin (Becton Dickinson), centrifuged for 10 min at approximately 4000*g*, and the plasma removed from the cells and stored frozen at –20°C until analysed for antifreeze activity.

Using a nanolitre osmometer (Clifton Technical Physics, Hartford, N.Y.), the freezing and melting points of the plasma samples were determined by observing, within each sample, the melting and freezing behaviour of a single ice crystal. By definition, the antifreeze proteins and glycoproteins depress the freezing point of any solution in which they are found while having very little effect on the melting point. The resulting difference (measured in degrees Celsius) between the freezing and melting points of a solution containing antifreeze is termed "thermal hysteresis" and is used as a direct measure of antifreeze activity (Kao et al. 1986).

In past studies, it has been found that during summer, when no antifreeze is present in the plasma, typical thermal hysteresis values of between 0.05 and 0.08°C are recorded using the above technique (Fletcher et al. 1987; Goddard et al. 1992). As winter approaches, antifreeze production is initiated. Previously, cod with thermal hysteresis values of 0.1°C and above have been considered antifreeze positive (Fletcher et al. 1987; Goddard et al. 1992). Thus, in this study, cod with thermal hysteresis values of 0.08°C and below were assigned to the "no antifreeze" group, while cod with thermal hysteresis values of 0.10°C and above were assigned to the "with antifreeze" category. Cod found to have thermal hysteresis levels of between 0.08 and 0.10°C were deemed ambiguous and not used in the statistical analyses. All results were analysed using statistical procedures outlined by Zar (1984).

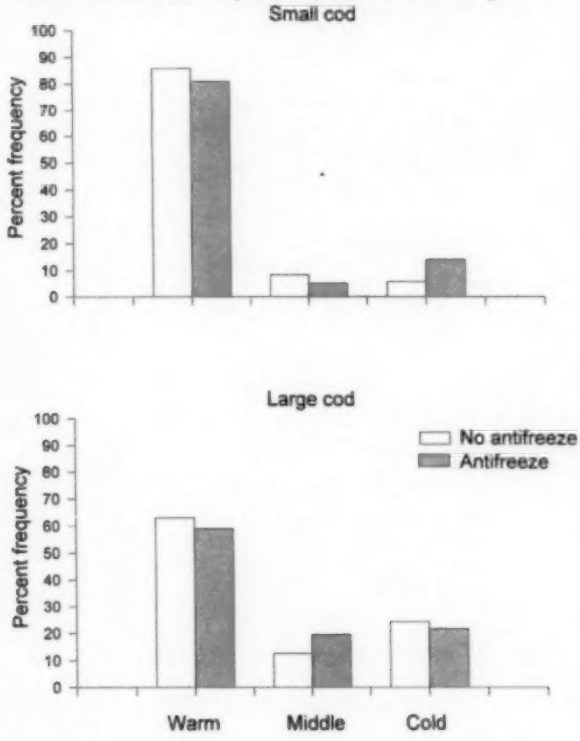
Results

Mean temperature occupied

There was no correlation (Pearson product moment correlation coefficient = 0.06, df = 41, p = 0.70) between blood plasma antifreeze levels (thermal hysteresis) and mean temperature occupied (Fig. 1). A similar lack of effect of antifreeze on mean temperature occupied was evident when cod were categorized based on size and the presence or absence of antifreeze rather than on the absolute antifreeze level. For large cod with and without antifreeze, the mean temperatures occupied ± 1 SD were 0.41 ± 0.20°C (n = 10) and 0.41 ± 0.25°C (n = 11), respectively. For small cod with and without antifreeze, the mean temperatures occupied ± 1 SD were 0.59 ± 0.40°C (n = 12) and 0.72 ± 0.22°C (n = 10), respectively. A two-way ANOVA showed no significant effect of

© 1997 NRC Canada

Fig. 2. Percent frequency with which cod in the four experimental groups occupied the warm (two compartments), middle (one compartment), and cold (two compartments) sections of the trough.



presence or absence of antifreeze on mean temperature occupied ($F = 0.53$, df = 1,39, $p = 0.47$) and no significant interaction between size and antifreeze ($F = 0.62$, df = 1,39, $p = 0.44$). There was, however, a significant effect of size on mean temperature occupied ($F = 7.87$, df = 1,39, $p = 0.008$), with large fish occupying a lower mean temperature (0.41 ± 0.28°C, mean ± 1 SD) than small fish (0.65 ± 0.29°C, mean ± 1 SD).

Distribution in the thermal gradient

To examine the distribution of cod in the thermal gradient, the frequency with which the fish in different antifreeze and size categories occupied the warm (two compartments), middle (one compartment), and cold (two compartments) sections of the trough was compared using a chi-square test. The possession of antifreeze proteins did not influence the frequency with which the large cod occupied different sections of the trough ($\chi^2 = 5.6$, df = 2, $p > 0.05$) (Fig. 2). However, the small cod possessing antifreeze did occur significantly more frequently in the cold area of the thermal gradient and less in the warm and middle sections than did the small cod with no antifreeze ($\chi^2 = 14.2$, df = 2, $p < 0.001$).

The size of the cod also appeared to influence their distribution within the gradient, with large cod occupying the cold and middle regions of the thermal gradient significantly more frequently than the small cod ($\chi^2 = 80.8$, df = 2, $p < 0.001$) (Fig. 2).

Transitions between compartments

The differences in distribution between large and small fish was further examined by comparing the amount of movement between compartments by the different-sized cod. Large cod made significantly more transitions from one compartment to another during the observation period than did small fish ($Z = 3.61$, $p < 0.02$, Mann–Whitney rank sum test). Mean number of transitions (±1 SD) was 20.4 ± 13.3 for large cod and 8.7 ± 7.6 for small cod. Small fish moved into the warmer parts of the trough and then made few movements into other compartments. Large fish, in contrast, while occurring most frequently in the warmer compartments, moved throughout the trough more than the small fish.

Seasonal changes have been reported to have an influence on the preferred temperatures of certain teleost fish, including cod (Tat'yankin 1974; McCauley and Huggins 1979; Clark and Green 1991). This study was carried out over a relatively short time period (approximately 2.5 mo), and no time trend in mean temperature occupied could be detected over the course of the experiment.

Discussion

Cod in all four groups showed a preference for the warmer compartments in the trough. This result is in accordance with laboratory studies on Atlantic cod and related species which reveal a preference for temperatures considerably in excess of those offered in this experiment (Bohle 1974; Jobling 1988; Schurmann and Steffensen 1992; Schurmann and Christiansen 1994). Field observations regarding cod distribution in the wild also suggest a definite preference for temperatures above 0°C (Taggart and Frank 1987; Rose et al. 1994). However, northern cod are found inhabiting subzero waters in the wild (Rose et al. 1994; Goddard et al. 1994), and the results of this experiment suggest possible mechanisms whereby both adult and juvenile cod may gradually become acclimated and adapted to subzero temperatures in winter when the need arises.

The presence of antifreeze had no significant effect on the responses of large fish to the temperature gradient. However, as a group, the large cod occupied significantly lower mean temperatures than the small cod. This result could be explained by the observation that thermal preference decreases with age in a variety of teleost species, including cod (Tat'yankin 1974; McCauley and Huggins 1979). However, we also observed that the large cod made a significantly greater number of transitions between compartments than the juveniles. Rate of thermal change in deep body structures of fish is inversely proportional to body size (Stevens and Sutterlin 1976). Thus, it is possible that forays into the cold water were less physiologically stressful to the large cod, resulting in their greater exploration of the trough and increased frequency of occurrence in the cooler compartments. No such difference in numbers of transitions, and hence activity, was found when comparing the two juvenile groups, suggesting that any differences between the small cod were not due simply to increased activity in the trough.

While the presence of low to medium levels of plasma antifreeze had no effect on the likelihood that large cod would make incursions into subzero waters, nevertheless, the large cod appeared comparatively ready to explore the subzero

© 1997 NRC Canada

areas of the trough. Time spent in sub-zero water promotes antifreeze production and its accumulation in the plasma (Fletcher et al. 1987; Goddard and Fletcher 1994). Thus, when faced with a declining temperature regime, for example when overwintering inshore, adult cod may build up their antifreeze levels in this manner, by swimming in and out of very cold water. By the time the water in the area they are inhabiting is uniformly cold, their plasma antifreeze levels may be sufficiently high to facilitate continuous existence at subzero temperatures.

Juvenile cod without antifreeze were found to avoid cold water. Due to their small body size, such explorations are probably more physiologically stressful than for the large cod. However, juveniles with the protection of plasma antifreeze did show an increased tendency to explore cold water. Juvenile northern cod produce antifreeze at temperatures of, at least, 2°C and below in winter (Goddard et al. 1992). Thus, although still preferring warmer temperatures, it may be that they explore waters at progressively lower temperatures as they produce increasingly high antifreeze levels with the onset of winter. Such incursions into low-temperature water would accelerate the accumulation of antifreeze in the plasma so that by the time waters in the overwintering area became uniformly subzero (e.g., in inshore areas), small cod would also be well equipped to tolerate such an environment.

Acknowledgements

Funding for this research was provided by the Northern Cod Science Program (NCSP), the Natural Sciences and Engineering Research Council of Canada (NSERC), and the Ocean Production Enhancement Network (OPEN), one of 15 Networks of Centres of Excellence supported by the Government of Canada.

References

Bohle, B. 1974. Temperaturpreferance hos torsk (*Gadus morhua* L.) Fisken Havet Ser. B**20**: 1–28.

Bull, H.O. 1936. Studies on conditioned responses in fishes. Part VII. Temperature perception in teleosts. J. Mar. Biol. Assoc. U.K. **21**: 1–28.

Clark, D.S., and Green, J.M. 1991. Seasonal variation in temperature preference of juvenile Atlantic cod (*Gadus morhua*), with evidence supporting an energetic basis for their diel vertical migration. Can. J. Zool. **69**: 1302–1307.

DeVries, A.L. 1988. The role of antifreeze glycopeptides and peptides in the freezing avoidance of Antarctic fishes. Comp. Biochem. Physiol. **90B**: 611–621.

Fissel, D.B., and Tang, C.L. 1991. Response of sea ice drift to wind forcing on the northeastern Newfoundland shelf. J. Geophys. Res. **96**: 18397–18409.

Fletcher, G.L., Slaughter, D., and Hew, C.L. 1982. Seasonal changes in the plasma levels of glycoprotein antifreeze, Na^+, Cl^-, and glucose in Newfoundland Atlantic cod (*Gadus morhua*). Can. J. Zool. **60**: 1851–1854.

Fletcher, G.L., King, M.J., and Kao, M.H. 1987. Low temperature regulation of antifreeze glycopeptide levels in Atlantic cod (*Gadus morhua*). Can. J. Zool. **65**: 227–233.

Goddard, S.V., and Fletcher, G.L. 1994. Antifreeze proteins: their role in cod survival and distribution from egg to adult. ICES mar. Sci. Symp. **198**: 676–683.

Goddard, S.V., Kao, M.H., and Fletcher, G.L. 1992. Antifreeze production, freeze resistance, and overwintering of juvenile northern Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **49**: 516–522.

Goddard, S.V., Wroblewski, J.S., Taggart, C.T., Howse, K.A., Bailey, W.L., Kao, M.H., and Fletcher, G.L. 1994. Overwintering of adult Northern Atlantic cod (*Gadus morhua*) in cold inshore waters as evidenced by plasma antifreeze glycoprotein levels. Can. J. Fish. Aquat. Sci. **51**: 2834–2842.

Jobling, M. 1988. A review of the physiological and nutritional energetics of cod, *Gadus morhua* L., with particular reference to growth under farmed conditions. Aquaculture, **70**: 1–19.

Kao, M.H., Fletcher, G.L., Wang, N.C., and Hew, C.L. 1986. The relationship between molecular weight and antifreeze polypeptide activity in marine fish. Can. J. Zool. **64**: 578–582.

Lear, W.H., and Green, J.M. 1984. Migration of the "northern" Atlantic cod and the mechanisms involved. *In* Mechanisms of migration in fishes. *Edited by* J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York. pp. 309–315.

Lear, W.H., Baird, J.W., Rice, J.C., Carscadden, J.E., Lilly, G.R., and Akenhead, S.A. 1986. An examination of factors affecting catch in the inshore cod fishery of Labrador and eastern Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. No. 1469.

McCauley, R.W., and Huggins, N.W. 1979. Ontogenetic and nonthermal seasonal effects on thermal preferenda of fish. Am. Zool. **19**: 267–271.

Morgan, M.J. 1993. Ration level and temperature preference of American plaice. Mar. Behav. Physiol. **24**:117–122.

Narayanan, S., Prinsenberg, S., and Colbourne, E.B. 1992. Overview of environmental conditions in 2J3KL NAFO subareas in 1991. NAFO SCR Doc. 92/6.

Petrie, B., Akenhead, S., Lazier, J., and Loder, J. 1988. The cold intermediate layer on the Labrador and Northeast Newfoundland shelves 1978–86. NAFO Sci. Counc. Stud. **12**: 57–69.

Rose, G.A., Atkinson, B.A., Baird, J., Bishop, C.A., and Kulka, D.W. 1994. Changes in distribution of Atlantic cod and thermal variations in Newfoundland waters, 1980–1992. ICES Mar. Sci. Symp. **198**: 542–552.

Rubinsky, B., Mattioli, M., Arav, A., Barboni, B., and Fletcher, G.L. 1992. Inhibition of Ca^{2+} and K^+ currents by "antifreeze" proteins. Am. J. Physiol. **262** (Regul. Integrative Comp. Physiol. **31**): R542–R545.

Schurmann, H., and Christiansen, J.S. 1994. Behavioural thermoregulation and swimming activity of two Arctic teleosts (Subfamily Gadinae) — the Polar cod (*Boreogadus saida*) and the Navaga (*Eleginus navaga*). J. Therm. Biol. **19**: 207–212.

Schurmann, H., and Steffensen, J.F. 1992. Lethal oxygen levels at different temperatures and the preferred temperature during hypoxia of the Atlantic cod, *Gadus morhua* L. J. Fish Biol. **41**: 927–934.

Simpson, A.C. 1953. Some observations on the mortality of fish and the distribution of plankton in the southern North Sea during the cold winter, 1946–1947. J. Cons. Perm. Int. Explor. Mer, **19**: 150–177.

Stevens, E.D., and Sutterlin, A.M. 1976. Heat transfer between fish and ambient water. J. Exp. Biol. **65**: 131–145.

Swain, D.P., and Kramer, D.L. 1995. Annual variation in temperature selection by Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence, Canada, and its relation to population size. Mar. Ecol. Prog. Ser. **116**: 11–23.

Taggart, C.T., and Frank, K.T. 1987. Coastal upwelling and *Oikopleura* occurrence ("slub"): a model and potential application to inshore fisheries. Can. J. Fish. Aquat. Sci. **44**: 1729–1736.

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

Tat'yankin, Y.V. 1974. The distribution of juvenile cod [*Gadus*

© 1997 NRC Canada

morhua morhua (L.)] pollock [*Pollachius virens* (L.)] and haddock [*Melanogrammus aeglefinus* (L.)] under temperature gradient conditions. J. Ichthyol. **114**: 1002–1011.

Templeman, W., and Fleming, A.M. 1956. The Bonavista longlining experiment, 1950–1953. Bull. Fish. Res. Board Can. No. 109.

Templeman, W., and Fleming, A.M. 1965. Cod and low temperature in St. Mary's Bay, Newfoundland. Int. Comm. Northwest Atl. Fish. Spec. Publ. **6**: 131–135.

Wroblewski, J.S., Bailey, W.L., and Howse, K.A. 1994. Observations of adult Atlantic cod (*Gadus morhua*) overwintering in nearshore waters of Trinity Bay, Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 142–150.

Zar, J.H. 1984. Biostatistical analysis. 2nd ed. Prentice-Hall, Inc., Englewood Cliffs, N.J.

© 1997 NRC Canada

Freezing resistance of caged Atlantic cod (*Gadus morhua*) during a Newfoundland winter

Garth L. Fletcher, J.S. Wroblewski, Martina M. Hickey, Brian Blanchard, Ming H. Kao, and Sally V. Goddard

Abstract: Closure of the Atlantic cod (*Gadus morhua*) fishery in Newfoundland has prompted considerable interest in cod aquaculture. However, the low temperatures and ice that characterize Newfoundland inshore waters during winter can be lethal to cod; thus, cage sites must be chosen with care. This study examines the overwintering conditions of caged cod located at two commercial aquaculture sites in southeast Newfoundland. Approximately 95% of the cod at these two sites overwintered successfully in landfast ice-covered cages, where water temperatures were below –1.2°C for at least 1 mo, and fell to minimum temperatures of –1.5°C at one site and –1.7°C at the other. Mean blood plasma freezing points of cod sampled from these sites were –1.2 and –1.11°C. Thus, cod can be overwintered in sea cages at temperatures below their freezing points (undercooled) — a situation that would normally be considered lethal, since contact with ice crystals would nucleate freezing in the undercooled cod. It is hypothesized that their survival was due to the thick covering of ice that prevented turbulence from driving surface ice crystals deep into the cage.

Résumé : La fermeture de la péche à la morue franche (*Gadus morhua*) à Terre-Neuve a suscité un intérêt considérable pour l'aquaculture de la morue. Cependant, les basses températures et les conditions glacielles qui caractérisent les eaux côtières de Terre-Neuve pendant l'hiver peuvent être mortelles pour la morue, d'où la nécessité de choisir avec soin les emplacements des cages. Cette étude se penche sur les conditions d'hivernation de morues en cages, dans deux sites d'aquaculture commerciale, au sud-est de Terre-Neuve. Environ 95 % des morues de ces deux établissements ont passé l'hiver avec succès dans des cages amarrées à la rive et recouvertes de glace, alors que la température de l'eau a été inférieure à –1,2°C pendant au moins 1 mo, et est tombée à des minimums de –1,5°C dans l'un des sites et –1,7°C dans l'autre. Les points de congélation moyens pour le plasma sanguin des morues échantillonnées dans ces sites étaient de –1,2 et de –1,11°C. Par conséquent, les morues peuvent passer l'hiver dans des cages marines à des températures inférieures à leur point de congélation (état de surfusion) — une situation qui normalement serait considérée comme fatale, étant donné que le contact avec les cristaux de glace pourrait entraîner la congélation chez les morues en état de surfusion. Nous avançons l'hypothèse que la survie des morues est due à l'épaisse couverture de glace empêchant que des remous ne fassent pénétrer les cristaux de glace de la surface profondément dans les cages.
[Traduit par la Rédaction]

Introduction

The collapse and closure of the northern Atlantic cod (*Gadus morhua*) fishery on the northeast coast of Newfoundland has prompted considerable interest in the prospect of cod aquaculture. However, since the subzero water temperatures and ice that characterize Newfoundland coastal waters during winter can be lethal to cod and most other fish, overwintering cage sites must be selected with great care (Davies et al. 1988; Wroblewski et al. 1993; deYoung and Sanderson 1995).

The blood and extracellular fluids of most teleost fish have freezing temperatures of -0.5 to -0.8°C, depending on their solute concentration (Holmes and Donaldson 1969). Since seawater temperatures can fall to -1.8°C before ice forms, fish residing in such waters can be undercooled by as much as 1°C and thus risk freezing if they come into contact with ice crystals (Scholander et al. 1957).

Fish such as the Atlantic salmon (*Salmo salar*) would always find such an environment lethal (Fletcher et al. 1988). Thus, with certain exceptions (e.g., Baie d'Espoir, Newfoundland), cage culture of this species in Atlantic Canada is largely restricted to the Passamaquoddy Bay, New Brunswick, area where temperatures rarely decline below 0°C. However, unlike salmon, Atlantic cod can increase their freeze resistance during winter by producing antifreeze glycopeptides (Hew et al. 1981; Fletcher et al. 1987; Goddard and Fletcher 1994).

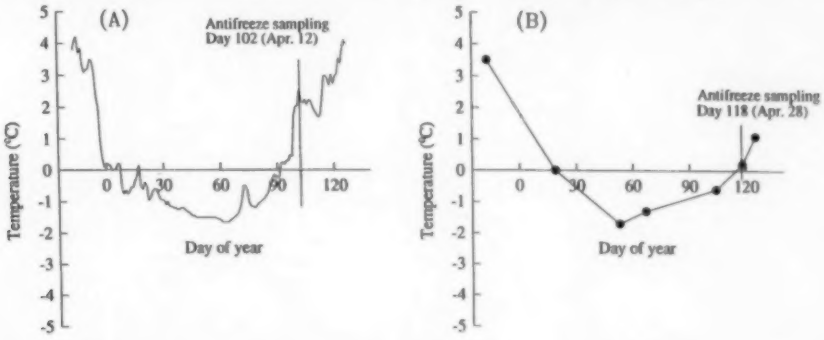
Adult and late juvenile Atlantic cod (>40 cm) synthesize antifreeze on a seasonal basis by responding to changes in water temperature. Antifreeze first appears in the blood when water temperatures decline through 0°C (early January). Peak concentrations are reached in March and disappear gradually when water temperatures rise above 0°C (Fletcher et al. 1987).

Received February 24, 1995. Accepted March 22, 1996.
J13440

G.L. Fletcher, M.H. Kao, and S.V. Goddard. Marine Sciences Research Laboratory, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada.
J.S. Wroblewski and M.M. Hickey. Fisheries Oceanography Group, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1C 5S7, Canada.
B. Blanchard. Seaforest Plantation, Co. Ltd., P.O. Box 517, Stn. C, St. John's, NF A1C 5K4, Canada.

© 1997 NRC Canada

Fig. 1. Temperatures at (A) Dunville and (B) Gooseberry Cove cage sites from December 1993 to April 1994. Temperatures were taken at 4 m depth at Dunville (continuous recording) and 5.4 m at Gooseberry Cove (point readings throughout the winter).



Antifreeze improves the freeze resistance of adult/late juvenile cod, but this resistance is limited. Previous studies have reported that cod with maximum antifreeze levels have mean plasma freezing points ranging from –1.1 to –1.35°C (Fletcher et al. 1987; Goddard and Fletcher 1994; Goddard et al. 1994). Thus, when antifreeze levels are at their highest, adult cod do not appear to be protected enough to survive the icy conditions typical of Newfoundland coastal waters, where temperatures can be as low as –1.8°C.

In recent years, commercial ventures have successfully overwintered adult cod in cages at several locations. However, water temperatures at the cage sites and the level of freeze resistance exhibited by the caged cod have never been documented.

The present study examines the freeze resistance of adult/late juvenile cod that have been held in sea cages for one to three winters.

Materials and methods

The conditions of overwintering cod in sea cages at two sites on the southeast coast of Newfoundland were studied over the winter of 1993–1994. The cages were located at Dunville, Placentia Bay, and in Gooseberry Cove, Trinity Bay. All fish studied were >43 cm and considered to be adult/late juveniles (Taggart et al. 1994).

The Dunville cod farm operated by Seaforest Plantation Co. Ltd. consisted of two circular cages, 15 m in diameter and approximately 11 m deep, located in an inlet with freshwater runoff. Cage 1 contained approximately 3000 fish that had been caught in Placentia Bay during the summer of 1993. Cage 2 contained approximately 1500 cod that had been caught on the east coast of the Avalon Peninsula (Petty Harbour/Maddox Cove area) during the summer of 1991 and had spent the previous two winters (1991–1992, 1992–1993) in sea cages.

The Gooseberry Cove cod farm was operated by Claude and Clarence Seward. Cod (approximately 1500) were held in a rectangular cage 9 × 11 × 5 m deep. These fish were caught in June 1992 near East Random Head, Trinity Bay, and had spent one winter (1992–1993) in the cage.

All cod were fed capelin or herring until November.

Temperature at the Dunville cod farm was continuously monitored at a depth of 4 m with a Hugren thermograph (MS-110SH) (resolution 0.01°C). Temperature profiles adjacent to the cages were taken on March 7 and April 12, 1994, at Dunville and on December 14, 1993, February 22, March 8, April 14, and April 28, 1994, at Gooseberry Cove using a Vemco Ltd. Sealog-TD temperature/depth logger (resolution 0.1°C) and a Seabird Electronics Inc. Seacat SBE 19-03 (resolution 0.001°C). The Seacat was also used to measure salinity. Both instruments were used on all dates except on February 22, 1994, when only a Sealog-TD was deployed at the Gooseberry Cove site.

The physiological condition of the cod was measured when the surface ice disappeared from the two sites in spring. Groups of cod were removed from each of the cages, weighed, measured, blood sampled, and returned to the cage. Blood samples of 1–2 mL were taken from a caudal blood vessel using 3-cm^3 syringes fitted with 21- or 23-gauge needles and were stored ice-cold in sodium heparinized Vacutainers (Becton Dickinson) until centrifugation. Following centrifugation (10 min at 4000*g*), the blood plasma was removed and stored frozen until analysis. Blood plasma freezing and melting points were determined using a nanolitre osmometer (Clifton Technical Physics, Hartford, N.Y.). In this method, the melting and freezing behaviour of a single ice crystal is observed under a microscope and thermal hysteresis is measured. Thermal hysteresis is the difference between the freezing and melting temperature of the plasma and is a direct measure of antifreeze activity (Kao et al. 1986).

Linear regression and statistical comparisons between groups (Student's *t*-test) were carried out using procedures described in Sokal and Rohlf (1987).

Results

Cage site conditions

Dunville

The water temperature (4 m depth) at the Dunville cage site declined below 0°C on January 10, 1994, reached a minimum value of –1.53°C on March 7, and warmed above 0°C on April 1, 1994 (Fig. 1A). Water temperatures were below –1.2°C for approximately 35 d from early February to the first week of March (Fig. 1A).

Surface ice formed during January 1994 and became landfast by the beginning of February. On March 7, the ice cover was approximately 33 cm thick. The site was ice free by April 12, 1994, at which time the low-salinity layer on the surface of the cage site was several metres thick (Fig. 2B).

The salinity profile taken on March 7 (Fig. 2B) indicated a salinity of 29 ppt below the ice layer. On April 12, 1994, the ice had melted and the low-salinity (<25 ppt) layer extended to a depth of 6 m.

On April 12, 1994 (when fish were sampled), water tem-

© 1997 NRC Canada

Fig. 2. (A) Temperature and (B) salinity profiles taken at the Dunville cage site on March 7, 1994 (*a*), and April 12, 1994 (*b*).

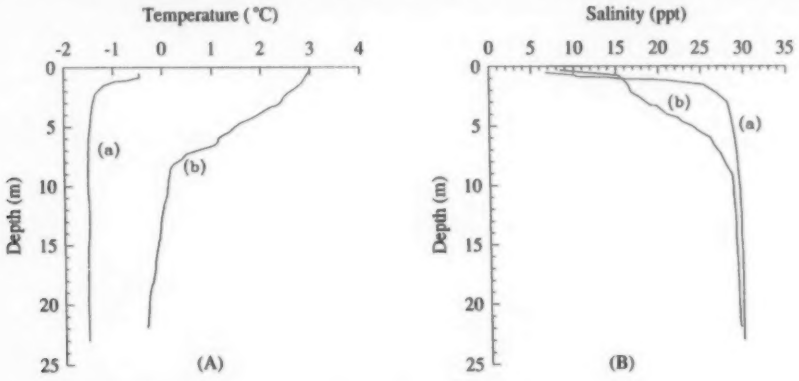
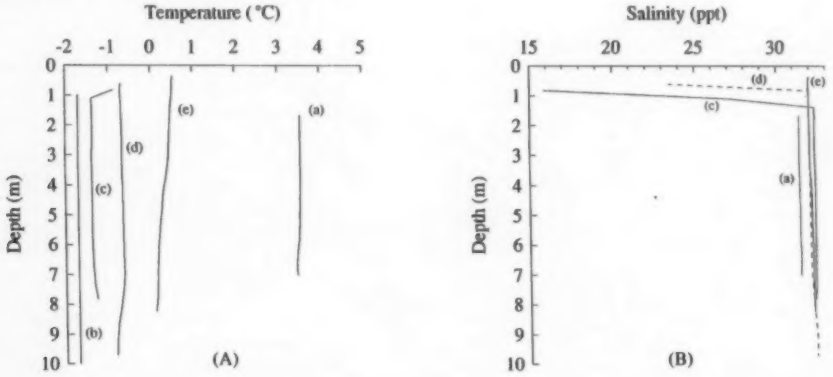


Fig. 3. (A) Temperature and (B) salinity profiles taken at the Gooseberry Cove cage site on December 14, 1993 (*a*), February 22, 1994 (*b*), March 8, 1994 (*c*), April 14, 1994 (*d*), and April 28, 1994 (*e*).



peratures adjacent to the cages (top to bottom) were +3 to 0°C, and salinities ranged from <15 to 28 ppt (Fig. 2).

Gooseberry Cove

Water temperatures at the Gooseberry Cove site declined below 0°C around January 20, and the lowest recorded temperature (–1.7°C) was measured on February 22, 1994. Temperatures were below –1.2°C for approximately 1 mo (around February 12 to March 11) and rose above 0°C during late April (Fig. 1B).

Ice covered the site in early February, and by February 22 was 38 cm thick. The ice began to melt on April 14, and by April 28 the site was ice free.

The salinity profiles taken between December 14, 1993, and April 28, 1994, indicated a salinity of approximately 32 ppt from a depth of 1 m and below. On April 28, 1994 (when fish were sampled), water temperatures in the vicinity of the cage (top to bottom) ranged from 0.5 to 0°C (Fig. 3).

Physiological condition of farmed cod

The commercial operators reported mortalities of 4.5% in Dunville cage 1, 6% in Dunville cage 2, and 5% in Gooseberry Cove.

The length and weight ranges for the cod sampled from the three cages were as follows: Dunville cage 1, 43.8–77.4 cm, 0.9–5.1 kg; Dunville cage 2, 45.6–70.5 cm, 1.1–3.3 kg; Gooseberry Cove, 49.0–76.5 cm, 1.8–5.4 kg. The mean body weight and length of the cod in Dunville cage 1 were significantly lower than those of the other two groups ($p < 0.01$ for each pairing).

Cod in all three cages produced antifreeze proteins (Table 1). No significant differences in plasma freezing points or thermal hysteresis values were observed between the cod at Dunville that were experiencing their first or third winter in a sea cage ($p > 0.05$).

Regression analysis of data for all cod in the Dunville cages combined ($N = 60$) showed that there was no correlation between thermal hysteresis and body length over the total length range of 43.8 – 77.4 cm ($p = 0.746$, $r^2 = 0.0018$). Slope of the regression (-4.62×10^{-4}) was not significantly different from zero.

Discussion

The temperature at which fish are in danger of freezing approximates the freezing point of their blood plasma. Although most fish from cold/temperate waters (cod included) can survive at temperatures below their freezing points, if they should

© 1997 NRC Canada

Table 1. Physiological condition of caged cod sampled in spring 1994.

Location and sampling date	*N*	Length (cm)	Weight (kg)	Plasma freezing point (°C)	Thermal hysteresis (°C)
Dunville cage 1, first winter, April 12, 1994	30	54.6±1.3	1.92±0.18	−1.22±0.01	0.50±0.01
Dunville cage 2, third winter, April 12, 1994	30	60.8±1.0	2.78±0.12	−1.19±0.02	0.46±0.02
Gooseberry Cove cage, second winter, April 28, 1994	42	61.1±0.8	3.12±0.12	−1.11±0.01	0.44±0.01

Note: *N* = numbers of cod sampled. Values are presented as means ± 1 SE.

contact ice while undercooled they will freeze and die (Scholander et al. 1957; Fletcher et al. 1986, 1988; Goddard and Fletcher 1994).

It is evident from the results of this study that despite the limited freeze resistance exhibited by the caged cod, the majority of them survived the winter in close proximity to ice at temperatures lower that the freezing points of their body fluids. The mean blood plasma freezing point data suggest that when the water temperatures were at their lowest, the cod were undercooled by 0.3 and 0.6°C for the Dunville and Gooseberry Cove sites, respectively. Since contacting ice would be lethal for cod at these temperatures, it must be concluded that such an event did not occur.

What does this study teach us about the conditions necessary to reduce the probability of cod freezing in sea cages during the winter? One important factor is the thick covering of landfast ice over the cages. At both sites, this ice was in place by the time water temperatures fell below −1.2°C and the majority of cod became undercooled (early February). By blocking turbulence in the upper water layer, the landfast ice would limit the downward mixing of ice crystals. Under these conditions, the positively buoyant ice crystals would remain near the top of the water column, and the cod would be able to avoid them by remaining deep in the cage.

A second factor, although one that does not appear to have played a role at the two sites during the winter of study, is salinity. Since the cod are in no danger of freezing until the water temperature declines below approximately −1.1°C, cages could be located in estuarine waters where the salinity is less than 20 ppt. At this lowered salinity, water temperatures can fall no lower than −1.08°C before freezing begins to take place (Gill 1982) and thus, cod would not be exposed to temperatures below their winter plasma freezing points. Atlantic cod are quite able to adapt to salinities considerably lower than this (Lambert et al. 1994). Thus, in the long term, areas of reduced salinity like that at Dunville would appear to be safer than areas of full-strength seawater for routinely overwintering cod.

Cod in all three sea cages had antifreeze levels typical of wild cod exposed to subzero temperatures for 2–3 mo in Trinity Bay (Goddard et al. 1994). In addition, the cod that had experienced three successive winters in a sea cage did not exhibit a greater ability to produce antifreeze than those that had experienced only one. Thus, retaining a caged brood stock over successive winters will not result in an improved ability to resist freezing.

Acknowledgements

We wish to thank Wade Bailey, Donald Best, Glen Best, Corey Blundell, Clarence and Claude Seward, and Kent Smedbol for assisting in field operations. Funding for this research was provided by the Canadian Centre for Fisheries Innovation, the Natural Sciences and Engineering Research Council of Canada (NSERC) with Fishery Products International Ltd. and National Sea Products Ltd. under NSERC's Research Partnerships Program, the Ocean Production Enhancement Network (OPEN), and the Northern Cod Science Program (NCSP).

References

Davies, P.L., Hew, C.L., and Fletcher, G.L. 1988. Fish antifreeze proteins: physiology and evolutionary biology. Can. J. Zool. **66**: 2611–2617.

deYoung, B., and Sanderson, B. 1995. The circulation and hydrography of Conception Bay, Newfoundland. Atmos.-Ocean, **95**: 135–162.

Fletcher, G.L., Kao, M.H., and Fourney, R.M. 1986. Antifreeze peptides confer freezing resistance to fish. Can. J. Zool. **64**: 1897–1901.

Fletcher, G.L., King, M.J., and Kao, M.H. 1987. Low temperature regulation of antifreeze glycopeptide levels in Atlantic cod (Gadus morhua). Can. J. Zool. **65**: 227–233.

Fletcher, G.L., Kao, M.H., and Dempson, J.B. 1988. Lethal freezing temperatures of Arctic char and other salmonids in the presence of ice. Aquaculture, **71**: 369–378.

Gill, A.E. 1982. Atmosphere ocean dynamics. Academic Press, New York.

Goddard, S.V., and Fletcher, G.L. 1994. Antifreeze proteins: their

© 1997 NRC Canada

role in cod survival and distribution from egg to adult. ICES Mar. Sci. Symp. **198**: 676–683.

Goddard, S.V., Wroblewski, J.S., Taggart, C.T., Howse, K.A., Bailey, W.L., Kao, M.H., and Fletcher, G.L. 1994. Overwintering of adult Northern Atlantic cod (Gadus morhua) in cold inshore waters as evidenced by antifreeze glycoprotein levels. Can. J. Fish. Aquat. Sci. **51**: 2834–2842.

Hew, C.L., Slaughter, D., Fletcher, G.L., and Joshi, S.B. 1981. Antifreeze glycoproteins in the plasma of Newfoundland Atlantic cod (Gadus morhua). Can. J. Zool. **59**: 2186–2192.

Holmes, W.N., and Donaldson, E.M. 1969. The body compartments and distribution of electrolytes. In Fish physiology. Vol. 1. Edited by W.S. Hoar and D.J. Randall. Academic Press, NewYork. pp. 1–89.

Kao, M.H., Fletcher, G.L., Wang, N.C., and Hew, C.L. 1986. The relationship between molecular weight and antifreeze polypeptide activity in marine fish. Can. J. Zool. **64**: 578–582.

Lambert, Y., Dutil, J.D., and Munro, J. 1994. Effects of intermediate and low salinity conditions on growth rate and food conversion of Atlantic cod (Gadus morhua). Can. J. Fish. Aquat. Sci. **51**: 1569–1576.

Scholander, P.F., van Dam, L., Kanwisher, J.W., Hammel, H.T., and Gordon, M.S. 1957. Supercooling and osmoregulation in Arctic fish. J. Cell. Comp. Physiol. **49**: 5–24.

Sokal, R.R., and Rohlf, F.J. 1987. Introduction to Biostatistics. W. H. Freeman and Co., New York.

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

Wroblewski, J.S., Collier, A., and Bailey, W. 1993. Ocean temperatures in the Random Island region of Trinity Bay, 1991–1992. The NSERC/Fishery Products International/National Sea Products Chair in Fisheries Oceanography, Data Rep. No. 1. Memorial University, St. John's, Nfld.

© 1997 NRC Canada

Does higher growth rate in Atlantic cod (*Gadus morhua*) at low salinity result from lower standard metabolic rate or increased protein digestibility?

J.-D. Dutil, Y. Lambert, and E. Boucher

Abstract: This study examines whether increased growth rate in Atlantic cod (*Gadus morhua*) at low salinity (14‰) can be accounted for by a reduction in standard metabolic rate (SMR) or by an increase in food assimilation (protein digestibility). Cod tolerate low salinity and exhibit higher growth rates at low salinity than in seawater. Differences between salinities are not associated with differences in food ingestion rates. SMR measured in cod exposed to low salinity and seawater (28‰) did not decrease or increase with changes in salinity. Similar results were obtained for cod with and without salinity acclimation. Weight loss in cod acclimated to salinity was similar at low salinity as in seawater. No difference in apparent protein digestibility was observed between cod acclimated to low salinity (14‰) and seawater. Estimates of protein digestibility were similar to those reported for cod in earlier studies. Higher growth rates and higher food conversion ratios at low salinity in cod must be attributable to uncontrolled or unmeasured factors such as spontaneous activity and swimming performance rather than to changes in SMR or in protein digestibility.

Résumé : Nous avons voulu déterminer si un meilleur taux de croissance à faible salinité (14‰) chez la morue franche (*Gadus morhua*) pouvait être imputable à une réduction du taux métabolique standard (TMS) ou un meilleur taux d'assimilation (digestibilité des protéines). La morue tolère bien les faibles salinités et son taux de croissance y est meilleur qu'en eau de mer. Cette différence entre les salinités n'est pas imputable à des différences dans le taux d'ingestion de nourriture. Le TMS n'a pas diminué chez les morues exposées à une faible salinité ni augmenté lorsque ces mêmes morues furent exposées de nouveau à l'eau de mer (28‰). Les résultats furent semblables chez des morues non acclimatées ou préacclimatées à la salinité. La perte de poids chez les morues pré-acclimatées à la salinité fut la même à faible salinité qu'en eau de mer. La digestibilité des protéines chez des morues acclimatées à l'une ou l'autre des salinités est semblable à celle mesurée par divers auteurs, mais nous n'avons constaté aucune différence entre les salinités. Les meilleurs taux de croissance à faible salinité doivent être attribuables à d'autres facteurs, par exemple le niveau d'activité spontanée ou la performance natatoire, plutôt qu'à des changements dans le TMS ou la digestibilité des protéines.

Introduction

Atlantic cod (*Gadus morhua*) have been shown to be tolerant to low salinity. Direct exposure of cod to 14 and 21‰ from 28‰ salinity resulted in only a negligible perturbation of the plasma electrolyte concentrations during any of the four seasons (Dutil et al. 1992). These perturbations were negligible compared with normal seasonal fluctuations in controls at 28‰. Marked decreases in plasma electrolytes were observed at 7‰ in spring and winter, i.e., at low temperatures (Dutil et al. 1992). Fish recovered to a new steady state, however, and no mortality occurred. Harden Jones and Scholes (1974), on the other hand, recorded two mortalities among 28 cod exposed to 7‰ salinity. No cod survived a short-term exposure to 3‰ salinity (Provencher et al. 1993). Odense et al. (1966) found similar results for cod exposed to a progressive reduction of water salinity over a period of 120 d.

Not only do cod tolerate low salinity, they also exhibit higher growth rates in brackish water (7 and 14‰) than in seawater (Lambert et al. 1994). These differences in growth rate among salinities were associated with differences in food conversion efficiencies rather than with differences in rate of food consumption. Lambert et al. (1994) hypothesized that higher growth rates and better food conversion efficiencies at 14‰ may have resulted from a reduction in the metabolic demand or from more efficient digestive and absorptive processes. The energetic cost of ion regulation is lowest in an isosmotic environment and it can be argued that enough energy will be spared to increase growth rate in reduced salinity (reviewed by Morgan and Iwama 1991). Environmental salinity will also modify drinking rates and could modify stomach evacuation rate, movement of food in the intestine, pH of gastric fluids, and food breakdown (DeSilva and Perera 1976; MacLeod 1977; Ferraris et al. 1986). This paper examines whether increased growth rate at 14‰ salinity in cod can be accounted for by a reduction in standard metabolic rate (SMR) or by an increase in protein digestibility.

Received December 20, 1994. Accepted September 26, 1995. J13228

J.-D. Dutil, Y. Lambert, and E. Boucher. Ministère des Pêches et des Océans, Institut Maurice-Lamontagne, C.P. 1000, Mont-Joli, QC G5H 3Z4, Canada.

© 1997 NRC Canada

Materials and methods

Experimental animals

Cod were caught by beam trawl in the St. Lawrence Estuary near Matane, Quebec, in June 1992 (metabolic rate experiments) and in June 1993 (food assimilation experiment). They were maintained in a flow-through system. Seawater was pumped from the St. Lawrence Estuary to reservoirs and delivered to the holding tank (13 m^3) at a flow rate of 25–50 $L \cdot min^{-1}$. Salinity varied in the range 28–30‰ and temperature between 5 and 10°C. Fluorescent lights were controlled by automatic timers adjusted weekly to follow the natural photoperiod at our latitude (48°N). Cod were fed capelin three times a week. Ration was above maintenance.

Standard metabolic rate

SMR was measured as the amount of oxygen consumed by a resting and fasting fish at 10°C. Two experiments were conducted, one in the summer and one in the autumn of 1992. For each experiment, four cod were placed individually in insulated respirometers made of acrylic and measuring 1 m in length and 15 cm in diameter. Fish ranged in length between 38 and 42 cm in both experiments and averaged 462 g during the first experiment and 512 g during the second experiment. Temperature regulation and aeration were carried out in a head reservoir. Temperature and flow rate were monitored continuously and adjusted to 9.8–10.2°C and 0.5 $L \cdot min^{-1}$, respectively. Dissolved oxygen was measured using a membrane electrode (Orion) calibrated in water-saturated air at 10°C. The calibration was checked against Winkler's method at the start of each experiment. The same electrode was used to measure dissolved oxygen concentration in the inlet and outlet tube of each respirometer. Readings were noted every 30 s over a period of 10 min. This was done once a day and each day roughly at the same time. Oxygen consumption was calculated as the difference in concentration between inlet and outlet, multiplied by flow rate and divided by fish weight. Fish weights were interpolated assuming a linear loss from initial to final weights. Results are expressed as milligrams of oxygen per hour per kilogram. Cod were not able to swim and did not struggle in the respirometers. Measured consumption was thus considered to be an estimate of SMR.

Cod in the summer experiment were not preacclimated to test salinities. Temperature acclimation (from 8 to 10°C) was done in the respirometers over 9 d while cod got used to their new surroundings. Following temperature acclimation, SMR was measured during 6 d at 28–29‰, 12 d at 14‰, and 8 d at 28–29‰ salinity. Changes in salinity took place in less than 1 h. Fish were not fed during acclimation and experimental periods.

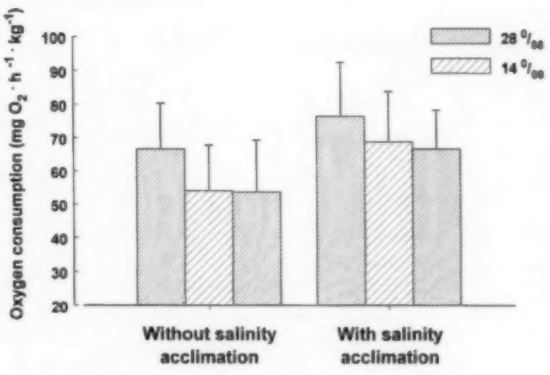
Cod in the autumn experiment were preacclimated to test salinities. Temperature acclimation (from 6 to 10°C) was done in the respirometers over 7 d. Then, SMR was measured during 10 d at 28–29‰. Following measurements, cod were returned to a 0.75-m^3 holding tank where they were fed at 10°C and 28–29‰. Four weeks later, they were reintroduced into the respirometers and were allowed 10 d to acclimate to 14‰ salinity. SMR was measured over the next 15 d at 14‰. Cod were then returned to the holding tank and allowed to feed and acclimate to 28–29‰ salinity for 2 wk at 10°C. Following that period, cod were transferred back into the respirometers for 10 d (29–30‰ salinity). SMR was then measured during the last 19 d at 29–30‰. The same fish were used throughout this experiment except for one which had to be replaced before making measurements at 14‰ salinity. The fish received no food while in the respirometers.

Food assimilation

This experiment took place in the summer of 1993. Twelve cod (521 ± 29 mm, 1308 ± 79 g) and 12 controls (513 ± 30 mm, 1254 ± 215 g) were abruptly exposed to 14 and 29–30‰ salinity, respectively. The cod were isolated in individual sections of one of six tanks (four cod in each 0.75-m^3 tank, three tanks for each salinity). While they acclimated to salinity, they were trained to ingest three capelin daily. Each day's meal was ingested within seconds. Training was carried on for 3 wk. Then, cod were not fed for 1 wk to ensure that no feces remained in the intestine.

Protein assimilation was assessed using chromium oxide (Cr_2O_3) as the nonabsorbable exogenous reference substance. The experiment was conducted at 10°C. Cr_2O_3 was added to a paste made of ground capelin and the paste was inserted in each capelin. Cr_2O_3 concentration in the paste was 6.4%. Labeled capelin contained 0.64 mg $Cr_2O_3 \cdot g$ wet $weight^{-1}$ or 2.17 mg Cr·g dry $weight^{-1}$. Cod received three Cr_2O_3-labeled capelin a day, i.e., 3.8% (14‰) and 4.0% (28‰) of body weight. The cod were fed for 6 d consecutively. They were killed on the seventh day by a blow on the head. Dissection was as described by Lied et al. (1982) except that gut segments were not washed with 0.9% NaCl solution. The gut was divided into six segments by ligations above the pyloric ceca, at the first cranial, first caudal, and second cranial bend of the intestine, at the ileorectal valve, and at the anus. The contents of each segment were dried to constant weight (65°C for 24 h) and frozen (–20°C). Protein content (N × 6.25) and Cr content were determined following Lied et al. (1982). Apparent protein digestibility was calculated as $100 - [(\text{proteins}_S/Cr_S)/(\text{proteins}_F/Cr_F)]$ where S is segment content and F is food content. Values are expressed on a dry-weight basis.

Fig. 1. Modifications of the SMR of four Atlantic cod (mean value with SD) at 10°C following changes in salinity from seawater (28‰) (left-hand bars) to diluted seawater (14‰) (middle bars), and back to seawater (right-hand bars), with or without salinity acclimation.



Results and discussion

Higher growth rates at 14‰ than at 28‰ in cod (Lambert et al. 1994) cannot be accounted for by differences in SMR (Fig. 1). SMR of cod did not differ significantly between periods ($P > 0.05$) in both acclimated and nonacclimated cod. Mean rates did not decrease nor increase following transfer from seawater to brackish water and back to seawater. Moreover, weight loss in the experiment with salinity acclimation was the same for cod at 14‰ (1.8 ± 0.5 $g \cdot d^{-1}$) as for cod in seawater (1.8 ± 0.2 $g \cdot d^{-1}$). Growth rates at 14‰ in Lambert et al. (1994) ranged from 14 to as much as 64% higher than in seawater depending on size, season, and feeding regime. SMR of cod would need to decrease considerably to account for such large increases in growth rate, since food ingestion was the same at 14‰ as in seawater (Lambert et al. 1994). Kirschner (1993) estimated that fish use 10–15% of their

© 1997 NRC Canada

Fig. 2. Day-to-day variations in SMR of Atlantic cod at 10°C following changes in salinity from seawater (28‰) to diluted seawater (14‰) and back to seawater, with or without salinity acclimation. Time in days does not include the period for salinity acclimation in the lower figure.

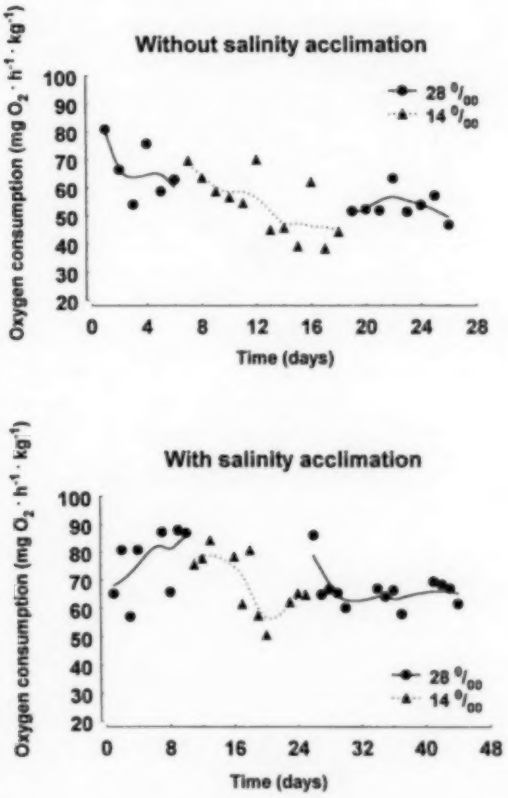
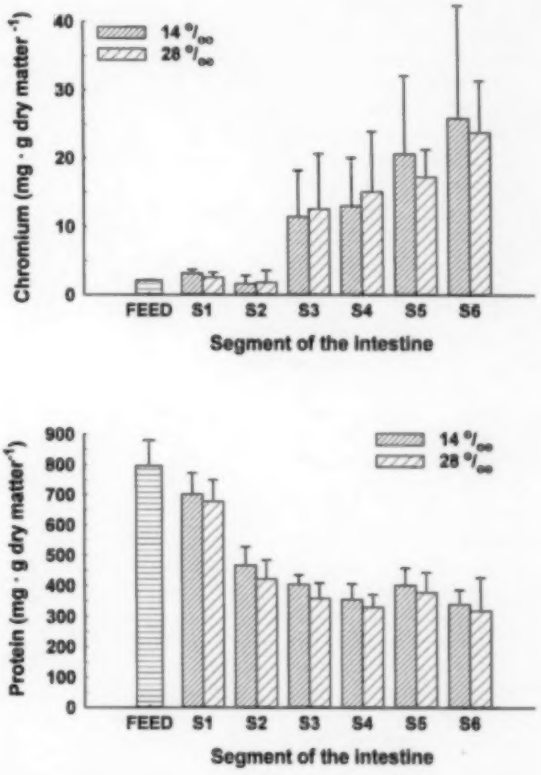


Fig. 3. Cr (as external indicator) and protein concentrations in the feed and in six segments of the digestive tract from the stomach (segment S1) to the rectum (segment S6) in Atlantic cod fed capelin at 10°C and under two salinity conditions, 14 and 28‰. Mean values with their SD are presented.


Chromium (mg · g dry matter^{-1})
14 ‰
28 ‰
FEED S1 S2 S3 S4 S5 S6
Segment of the intestine
Protein (mg · g dry matter^{-1})
14 ‰
28 ‰
FEED S1 S2 S3 S4 S5 S6
Segment of the intestine

standard metabolism for osmotic regulation. His estimate was based on calculations of ATP demand for regulatory mechanisms. Should cod reduce metabolic rate by 15%, they would not save enough energy to account for the measured difference in growth rate between salinities (Lambert et al. 1994). Proportions higher than 15% have been calculated from measures of oxygen consumption in two other fish species (Rao 1968; Farmer and Beamish 1969). Morgan and Iwama (1991) concluded, however, that salinities promoting lower standard metabolic rate and higher growth rate were not the same for different species and different life-history stages. The metabolic rate of many marine species was unaffected by salinity whereas several estuarine and marine species had a lower metabolic rate in isotonic salinity, in freshwater, or in seawater. Based on average SMR values in our studies (Fig. 1), no decrease occurred in isotonic salinity in the summer or autumn experiments.

The lowest daily SMR values were observed at 14‰ in both the summer and autumn experiments (38 and 50 mg $O_2 \cdot h^{-1} \cdot kg^{-1}$). This is much less than reported in earlier studies for cod in full seawater. SMR estimates in the literature, once adjusted for size (500 g) (Steffensen et al. 1994) and

Table 1. Apparent protein digestibility in six segments of the gastrointestinal tract from the stomach (S1) to the rectum (S6) in Atlantic cod fed capelin at 10°C and under two salinity conditions.

Segment of intestine	14‰ salinity	28‰ salinity
S1 (stomach)	38.4 ± 11.0	25.1 ± 23.6
S2	−10.9 ± 69.9	−39.7 ± 159.4
S3	86.7 ± 9.5	86.6 ± 12.8
S4	88.9 ± 9.3	91.7 ± 5.9
S5	93.0 ± 4.2	93.4 ± 3.6
S6 (rectum)	94.7 ± 3.9	94.9 ± 5.7

Note: Digestibility is calculated as the quotient of the ratios between protein and Cr (external indicator) concentrations in the feed and in the intestinal segments of 12 cod at 14‰ and 12 cod at 28‰.

temperature (10°C) (Saunders 1963), vary from 64 mg (Sundnes 1957) to 74 mg (Saunders 1963), 75 mg (Bushnell et al. 1994), 80 mg (12°C) (Edwards et al. 1972), and 86 mg $O_2 \cdot h^{-1} \cdot kg^{-1}$ (Soofiani and Hawkins 1982). Values derived from exercised cod were not lower than those derived from

© 1997 NRC Canada

resting cod: roughly 54 mg $O_2 \cdot h^{-1} \cdot kg^{-1}$, based on an SMR value of 36 mg for a 1-kg cod at 2°C (Nelson et al. 1994), and roughly 66 mg $O_2 \cdot h^{-1} \cdot kg^{-1}$, based on an SMR value of 61 mg for a 155-g cod at 4.5°C (Steffensen et al. 1994). SMR estimates in this study averaged 56 and 70 mg $O_2 \cdot h^{-1} \cdot kg^{-1}$ in the first and second experiment, respectively.

The decline in SMR during the course of the summer experiment suggests that cod were acclimating to salinity or to confinement (first and second period). SMR decreased following transfer to brackish water (14‰), but failed to increase after salinity was increased (third period) in both acclimated and nonacclimated cod (Fig. 2). Providing a longer period of acclimation to salinity would not have changed our conclusions. Salinity acclimation, particularly in summer, occurs in a much shorter period than the period of acclimation used in our study (Dutil et al. 1992). Handling stress, on the other hand, may explain differences between experiments. Minimal SMR values were reached roughly 20 d after the introduction of cod in the respirometers (summer experiment). Handling may have increased SMR in the autumn experiment because salinity acclimation was conducted outside the respirometers before each series of measurements. Although the cod were introduced in the respirometers as long as 7–10 d before measuring SMR, a longer period may have reduced SMR and day-to-day fluctuations. Increased SMR due to stress could also occur in situations where cod are forced to swim in order to estimate SMR from extrapolation to zero activity (Smit 1965). Differences in weight at length may also have contributed to the observed differences between experiments: cod in the autumn experiment had a heavier mass for the same length than cod in the summer experiment which would contribute to a higher metabolic rate in the autumn experiment.

Apparent protein digestibility was very similar between salinities and did not explain the differences in growth rate found by Lambert et al. (1994). Cr concentration increased as protein concentration decreased along the digestive canal (Fig. 3) on both a dry- and wet-weight basis ($P < 0.0001$). No difference was observed between salinities except for protein concentration on a dry-weight basis ($P < 0.01$). This difference was also significant when the analysis was restricted to the last four gut segments ($P = 0.02$). Differences in protein concentration did not result in significant differences in protein assimilation between salinities: 90.8% at 14‰ and 91.6% in seawater for segments 3–6, and 94.7% at 14‰ and 94.9% in seawater for segment 6 ($P > 0.05$) (Table 1). Protein assimilation took place in the anterior part of the intestine, and protein concentration decreased slowly from segment 3 to segment 6. Protein digestibility increased to 87% in segment 3 and reached a maximum value of 95% in segment 6. These values are close to levels reported by Lied et al. (1982) for cod fed capelin at 8°C in full seawater. These authors recommended that samples should be taken from segment 5. Protein digestibility estimated from segment 5 samples was 93% in both studies. Lie et al. (1988) also found values above 90%, although on small cod at higher temperatures. DeSilva and Perera (1984) also concluded that salinities in the range 0–10‰ had no significant effect on digestibility in *Sarotherodon niloticus* fry. However, apparent digestibility of N (protein) in Atlantic salmon (*Salmo salar*) was observed to be 9–10% lower in seawater-adapted smolts compared with freshwater-adapted smolts (Usher et al. 1990). To our knowledge, no other study has examined the influence of salinity on protein digestibility in fish.

Higher growth rates and higher food conversion efficiencies at 14‰ (Lambert et al. 1994) must be attributable to uncontrolled or unmeasured factors rather than to changes in SMR or protein digestibility. Activity level was highest in full seawater in the euryhaline milkfish (*Chanos chanos*) (Swanson 1992). Differences in metabolic rate and growth rate were mainly attributable to salinity-related variations in spontaneous activity. Swimming performance was best in isotonic seawater in juvenile common snook (*Centropomus undecimalis*). Isotonic conditions promoted a lower maintenance cost, a higher aerobic scope, and no increase in lactate at high swimming speeds (Pérez-Pinzón and Lutz 1991). The cost of ion-osmotic regulation may be more easily measured or may actually increase in situations of high energy demand such as would be the case in satiation feeding experiments (Soofiani and Hawkins 1982), during exercise (Tang et al. 1994), in tests of tolerance, and in stressful situations in general. Such situations may result in a costly failure of ion and osmotic regulation mechanisms. This failure could be prevented in euryhaline species by a reduction of food consumption, a reduction of maximum swimming speed, avoidance of extreme situations, or a reduced performance of intermediary metabolic mechanisms. These responses are common in fish exposed to low dissolved oxygen tensions and would be consistent with Lambert et al.'s (1994) results that growth rates are higher at 14‰ than in seawater.

Acknowledgements

The authors wish to thank Sylvain Chartrand, who designed and prepared the data acquisition system for the metabolic rate experiments, Bernard Chenard for his advice during this project, Mario Péloquin and Pierre Sylvestre for their technical assistance, and Claudie Vigneault for the analysis of Cr and protein in the food assimilation experiment. This project was supported by the Programme fédéral de développement des pêches du Québec and by regular funding from the Department of Fisheries and Oceans (Canada).

References

Bushnell, P.G., Steffensen, J.F., Schurmann, H., and Jones, D.R. 1994. Exercise metabolism in two species of cod in arctic waters. Polar Biol. **14**: 43–48.

DeSilva, S.S., and Perera, P.A.B. 1976. Studies on the young grey mullet, *Mugil cephalus*. I— Effects of salinity on food intake, growth and food conversion. Aquaculture, **7**: 327–338.

DeSilva, S.S., and Perera, M.K. 1984. Digestibility in *Sarotherodon niloticus* fry: effect of dietary protein level and salinity with further observations on variability in daily digestibility. Aquaculture, **38**: 293–306.

Dutil, J.-D., Munro, J., Audet, C., and Besner, M. 1992. Seasonal variation in the physiological response of Atlantic cod (*Gadus morhua*) to low salinity. Can. J. Fish. Aquat. Sci. **49**: 1149–1156.

Edwards, R.R.C., Finlayson, D.M., and Steele, J.H. 1972. An experimental study of the oxygen consumption, growth, and metabolism of the cod (*Gadus morhua*). J. Exp. Mar. Biol. Ecol. **8**: 299–309.

Farmer, G.J., and Beamish, F.W.H. 1969. Oxygen consumption of

© 1997 NRC Canada

Tilapia nilotica in relation to swimming speed and salinity. J. Fish. Res. Board. Can. **26**: 2807–2821.

Ferraris, R.P., Catacutan, M.R., Mabelin, R.L., and Jazul, A.P. 1986. Digestibility in milkfish, *Chanos chanos*: effects of protein source, fish size and salinity. Aquaculture, **59**: 93–105.

Harden Jones, F.R., and Scholes, P. 1974. The effect of low temperature on cod, *Gadus morhua*. J. Cons. Int. Explor. Mer, **35**: 258–271.

Kirschner, L.B. 1993. The energetics of osmotic regulation in ureotelic and hypoosmotic fishes. J. Exp. Zool. **267**: 19–26.

Lambert, Y., Dutil, J.-D., and Munro, J. 1994. Effects of intermediate and low salinity conditions on growth rate and food conversion of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **51**: 1569–1576.

Lie, O., Lied, E., and Lambertsen, G. 1988. Feed optimization in Atlantic cod (*Gadus morhua*): fat versus protein content in the feed. Aquaculture, **69**: 333–341.

Lied, E., Julshamn, K., and Braekkan, O.R. 1982. Determination of protein digestibility in Atlantic cod (*Gadus morhua*) with internal and external indicators. Can. J. Fish. Aquat. Sci. **39**: 854–861.

MacLeod, M.G. 1977. Effects of salinity on food intake, absorption, and conversion in the rainbow trout *Salmo gairdneri*. Mar. Biol. **43**: 93–102.

Morgan, J.D., and Iwama, G.K. 1991. Effects of salinity on growth, metabolism, and ion regulation in juvenile rainbow and steelhead trout (*Oncorhynchus mykiss*) and fall chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **48**: 2083–2094.

Nelson, J.A., Tang, Y., and Boutilier, R.G. 1994. Differences in exercise physiology between two Atlantic cod (*Gadus morhua*) populations from different environments. Physiol. Zool. **67**: 330–354.

Odense, P., Bordeleau, A., and Guilbault, R. 1966. Tolerance levels of cod (*Gadus morhua*) to low salinity. J. Fish. Res. Board Can. **23**: 1465–1467.

Pérez-Pinzón, M.A., and Lutz, P.L. 1991. Activity related cost of osmoregulation in the juvenile snook (*Centropomus undecimalis*). Bull. Mar. Sci. **48**: 58–66.

Provencher, L., Munro, J., and Dutil, J.-D. 1993. Stress and osmotic performance of Atlantic cod at 1–7 g/L water salinity. Aquaculture, **116**: 219–231.

Rao, G. 1968. Oxygen consumption of rainbow trout in relation to activity and salinity. Can. J. Zool. **46**: 781–786.

Saunders, R.L. 1963. Respiration of the Atlantic cod. J. Fish. Res. Board Can. **20**: 373–386.

Smit, H. 1965. Some experiments on the oxygen consumption of goldfish (*Carassius auratus*) in relation to swimming speed. Can. J. Zool. **43**: 623–633.

Soofiani, N.M., and Hawkins, A.D. 1982. Energetic costs at different levels of feeding in juvenile cod, *Gadus morhua*. J. Fish Biol. **21**: 577–592.

Steffensen, J.F., Bushnell, P.G., and Schurmann, H. 1994. Oxygen consumption in four species of teleosts from Greenland: no evidence of metabolic cold adaptation. Polar Biol. **14**: 49–54.

Sundnes, G. 1957. Notes on the energy metabolism of the cod (*Gadus callarias*) and the coalfish (*Gadus virens*) in relation to body size. Fiskeridir. Skr. Ser. Havunders. **9**: 3–10.

Swanson, C. 1992. Culture of a euryhaline fish: effects of salinity on metabolism, activity, and growth in the milkfish, *Chanos chanos*. Aquaculture '92: Growing toward the 21st century, 21–25 May 1992, Orlando, Fla. Summary.

Tang, Y., Nelson, J.A., Reidy, S.P., Kerr, S.R., and Boutilier, R.G. 1994. A reappraisal of activity metabolism in Atlantic cod (*Gadus morhua*). J. Fish Biol. **44**: 1–10.

Usher, M.L., Talbot, C., and Eddy, F.B. 1990. Effects of transfer to seawater on digestion and gut function in Atlantic salmon smolts (*Salmo salar*). Aquaculture, **90**: 85–96.

© 1997 NRC Canada

Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)?

Yvan Lambert and Jean-Denis Dutil

Abstract: This study examined whether simple indicators of condition in individual Atlantic cod (*Gadus morhua*) are related to biochemical composition and energy content for the whole range of conditions potentially observed in natural populations. The energy content of muscle was largely associated with its protein content, while liver energy content mainly consisted of lipids. Accurate predictions of muscle and liver energy content can also be made from the measurement of their water content. Relationships between energy content, water content, and simple measures such as condition factor and hepatosomatic index provide a fast and accurate assessment of seasonal changes in total available energy reserves in cod. These indices could advantageously be used to monitor the status and recovery of cod stocks and to ensure improved management of that resource.

Résumé : Dans cette étude, nous relions des indicateurs simples de la condition des morues franches (*Gadus morhua*) à leur composition biochimique et leur contenu énergétique et ce pour tous les niveaux de condition pouvant être observés en conditions naturelles. Le contenu en énergie du muscle est largement associé à son contenu en protéines alors que celui du foie est essentiellement relié à son contenu en lipides. Les contenus en protéines du muscle et en lipides du foie sont fortement correlés au contenu énergétique de leur tissu respectif. Des prédictions très précises du contenu énergétique du muscle et du foie peuvent être obtenues par une simple mesure de leur contenu en eau. Les relations qui existent entre les contenus en eau et en énergie ainsi que des mesures simples de condition tel le facteur de condition et l'indice hépato-somatique sont un outil précis et rapide pour mesurer et monitorer les changements saisonniers dans les réserves d'énergie de la morue. Ces indices pourraient avantageusement être utilisés pour suivre l'état et le rétablissement des stocks de morue et assurer une meilleure gestion de cette ressource.

Introduction

Atlantic cod (*Gadus morhua*), like many fish species, shows seasonal patterns in its biochemical composition and energy content in association with feeding intensity, migration, maturation, and spawning. Several studies have demonstrated relationships between biochemical composition, growth, maturation, fecundity, and egg size (Love 1958, 1960, 1970; Eliassen and Vahl 1982*a*, 1982*b*; Holdway and Beamish 1984; Kjesbu et al. 1991; Lambert et al. 1994). Knowledge of variability in the biochemical composition of cod can thus provide useful information on the ability of cod to cope with fluctuating environmental conditions.

Cod is considered to be a lean fish, lipid content of the body musculature representing less than 1% of the muscle wet weight (Bogucki and Trzesinski 1949; Dambergs 1964; Jangaard et al. 1967; Eliassen and Vahl 1982*b*; Holdway and Beamish 1984; Jobling 1988; Lie et al. 1988; Kjesbu et al. 1991). Body musculature in cod as in the other Gadidae is the main protein depot, while lipid reserves are primarily stored in the liver (Bogucki and Trzesinski 1949; Love 1970; Eliassen and Vahl 1982*a*; Jangaard et al. 1967; Holdway and Beamish 1984; Black and Love 1986; Lie et al. 1988; Jobling et al. 1991; Kjesbu et al. 1991; Dos Santos et al. 1993; Hemre et al. 1993). Changes in the lipid content of the liver and in the protein and water content of the muscle are believed to reflect changes in the seasonal patterns of the biochemical composition of cod (Love 1958, 1960, 1962; Ironside and Love 1958). The cited literature shows that protein and water content of the muscle can vary between 10 and 19% and between 79 and 88%, respectively, while liver lipid content can vary between 2 and 75%. Analysis of energy, lipid, and water content of whole cod indicates that these constituents are correlated, so that accurate predictions of each component can be obtained from the measurement of any of the others (Holdway and Beamish 1984).

Some biochemical constituents of cod appear to be correlated with their general condition. Love (1958, 1962) for example, observed that cod that were very emaciated in appearance had a liver lipid content of less than 5% and a muscle water content of more than 83%. Fish that were considered as "normal" had a muscle water content of 80% and a corresponding liver lipid content of more than 25%. There are indications that seasonal changes in some condition indices can be used to quantify the general condition of cod. In many studies, different forms of the condition factor and liver index have been used as indicators of the well-being, nutritional sta-

Received December 20, 1994. Accepted June 21, 1995.
J13229

Y. Lambert and J.-D. Dutil. Ministère des Pêches et des Océans, Institut Maurice-Lamontagne, C.P. 1000, Mont-Joli, QC G5H 3Z4, Canada.

© 1997 NRC Canada

tus, previous nutritional history, and growth of cod (Love 1958,1962; Harden Jones and Scholes 1974; Holdway and Beamish 1984; Hawkins et al. 1985; Pedersen and Jobling 1989; Jobling et al. 1991; Dos Santos et al. 1993; Foster et al. 1993). These observations suggest that relationships may exist between condition indices and biochemical constituents of cod. In pollock (*Pollachius virens*), which stores its energy reserves in the same way as cod, the liver index is well correlated with lipid content of the liver and with water content of both liver and muscle (Jensen 1979). On the basis of these relationships, Jensen concluded that the liver index is an excellent measure of condition in pollock. In European plaice (*Pleuronectes platessa*), the condition factor has been identified as a good indicator of the proximate composition and energy content of wild fish (Costopoulos and Fonds 1989). However, in none of the studies on the biochemical composition and condition of cod has the full range of values for each component been obtained. This is especially true for cod with lower energy content and poor condition. The only data available are those of Love (1958) and Black and Love (1986) which are based on a few individuals. For that reason, no studies have fully examined the relationships between biochemical constituents of cod and different condition indices assumed to reflect the well-being of cod.

The recent collapse of many cod stocks in the Northwest Atlantic has fostered an interest in assessing individual condition along with abundance as part of the process of stock conservation and management. Because routine measures of biochemical composition or energy content are time consuming, simple indices related to biochemical composition or energy content are required to assess the status of wild fish. Because cod experience large variations in condition between regions, seasons, or years, these indices have to be validated for a wide range of condition values. This is particularly so as the recent decline in the biomass of the cod stock in the northern Gulf of St. Lawrence was associated with more extreme levels of condition (Fréchet et al. 1994).

This study examined whether simple indicators of condition are related to the biochemical composition and energy content of cod for the whole range of conditions that can be observed in natural populations. More specifically, biochemical composition and interrelationships between biochemical components of cod for a broad range of energy content were examined. Relationships between energy content and simple condition indices were also established to evaluate the potential use of condition indices to monitor and quantify seasonal changes in the energy reserves of cod.

Materials and methods

Biochemical composition, energy content, and condition indices used to describe the variability in the energy reserves of cod and the interrelationships between these components were obtained from different data sources. Biochemical composition was evaluated from two experiments conducted in 1991, while relationships between biochemical composition and condition indices were obtained from a starvation experiment realized in 1994 and from samples of wild cod collected in the northern Gulf of St. Lawrence between 1993 and 1994.

Biochemical composition of cod was evaluated from two growth experiments conducted in 1991 at three different salinities (Lambert et al. 1994). Fish from all salinities were included, as the salinity has no significant effect on their chemical composition (Lambert et al. 1994). Fish in each experiment were fed to satiation either once a week or three times weekly. Cod were sampled at the beginning and the end of each experiment. Various length and weight measurements were made and tissue samples were collected from each fish for the determination of their biochemical composition (Lambert et al. 1994). With such feeding schedules, a broad range in biochemical composition and energy content was obtained. Biochemical composition of muscle and liver were examined, as these tissues represent the bulk of the energy reserves in cod (Love 1970; Holdway and Beamish 1984; Hemre et al. 1993). For each tissue, duplicate analyses of water, lipid, and protein content were performed on homogenates. Glycogen content was only analyzed for the liver, since its concentration in the muscle of cod is ordinarily less than 0.4% of the wet weight (Black and Love 1986; Kjesbu et al. 1991). A detailed description of the analytical methods is given in Lambert et al. (1994). Energy content in each tissue was calculated by applying energy equivalents of 39.5, 23.6, and 17.1 kJ/g for lipid, protein, and glycogen, respectively (Kleiber 1975). The relative importance of lipid, protein, and glycogen content in the muscle and liver was assessed by comparing their respective percentages over a wide range of energy content for each tissue. The contribution of each component to the total energy content of tissues was also calculated.

Relationships between biochemical composition and condition indices were evaluated from two sets of data, covering a wide range of values for condition and energy content. Data were obtained from a starvation experiment conducted in our laboratory in 1994 and from samples of wild cod collected in the northern Gulf of St. Lawrence. In the starvation experiment, cod were starved for 150–250 d at temperatures between 0 and 10°C to ensure that minimal energy reserves had been reached. Actually, some cod died of starvation and others were killed as they were considered moribund. Cod that scarcely responded to external stimuli and that had difficulty maintaining equilibrium were defined as being moribund. Six samples of around 50 cod each were also obtained at intervals of roughly 2 mo from the northern Gulf of St. Lawrence. These samples were collected between June 1993 and May 1994 to cover the annual cycle of energy content. Cod in the starvation experiment measured between 40 and 55 cm in length and cod sampled in the northern Gulf of St. Lawrence ranged between 30 and 50 cm.

Several length and weight measurements and several tissue samples were collected on all fish used in the starvation experiment and on all fish collected in the Gulf of St. Lawrence. For each fish, fork length (millimetres) was measured and total weight (±1 g) and liver, gonad, and stomach content weights (±0.1 g) were taken. Muscle weight was estimated as the eviscerated carcass weight with head removed. Two condition indices were also used, the condition factor and the hepatosomatic index HSI). Condition factor was expressed as Fulton's condition factor (K) with the formula

$$K = 100 \cdot W/L^3$$

where W is somatic weight (grams) and L is fish length (centimetres) (Bagenal 1978). Somatic weight was calculated as the total weight of fish less gonad and stomach content weights. Somatic weight was selected, as feeding intensity and gonad maturation can vary significantly and independently of condition between seasons and within and between stocks. Somatic weight is also a more precise reflection of condition, as available energy reserves of an individual will be located in somatic tissues (somatic cells as opposed to germ cells). HSI was calculated as

$$\text{HSI} = (\text{LW}/W) \cdot 100$$

where LW and W represent liver weight and somatic weight (grams), respectively. These condition indices were selected for their simplicity and because they have been identified as potentially good indicators of the general well-being of cod (Jangaard et al. 1967; Holdway and Beamish 1984; Pedersen and Jobling 1989; Dos Santos et al.

© 1997 NRC Canada

Fig. 1. Variations in the protein and lipid composition of muscle in relation to changes in muscle energy content in cod. Muscle proteins and lipids are expressed as percentages of wet weight and as percentages of energy content.

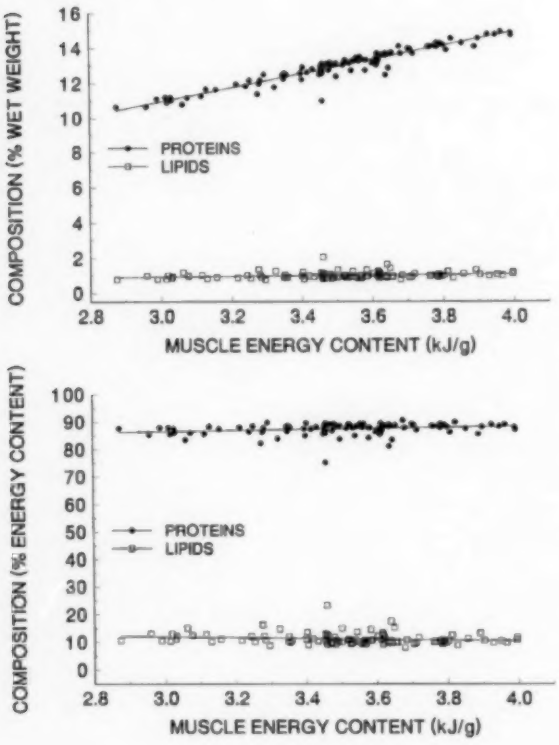
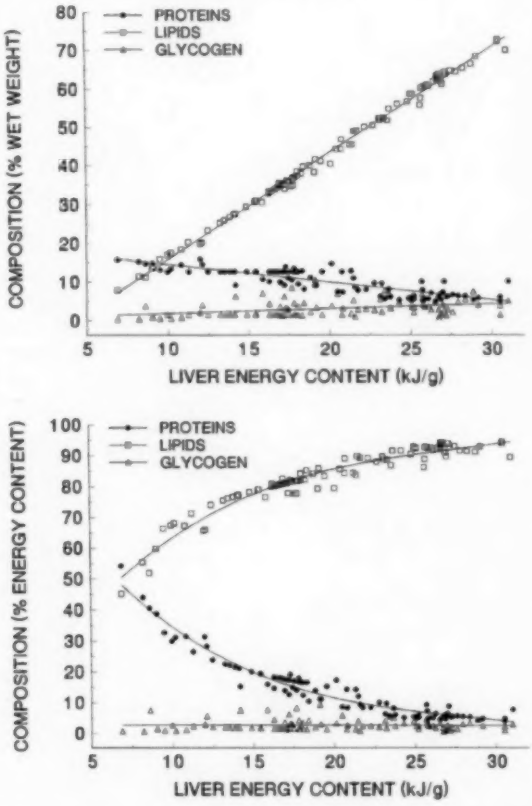


Fig. 2. Variations in the protein, lipid, and glycogen composition of liver in relation to changes in liver energy content in cod. Liver proteins, lipids, and glycogen are expressed as percentages of wet weight and as percentages of energy content.



1993; Foster et al. 1993). The importance of maturation and the associated energy investment in the gonads were not examined here because reproductive tissue, although influencing the condition of cod, does not represent energy reserves readily available to the fish.

Muscle and liver samples were taken to determine their water and energy content. Water content was determined by drying tissue samples to constant weight at 65°C and energy content by combusting tissue samples in an oxygen bomb calorimeter (Parr, model 1261).

Muscle and liver energy content were expressed on both a relative and an absolute basis. Specific energy content was calculated as the quantity of energy (kilojoules) per gram of fresh tissue and total energy content as the product between specific energy content and tissue mass.

Results

Biochemical composition

Muscle energy content was largely associated with its protein content, while liver energy content mainly consisted of lipids. Proteins represented 10–14% of the muscle composition by wet weight, while lipids represented only 1% (Fig. 1). Glycogen concentrations as reported in the literature (Black and Love 1986; Kjesbu et al. 1991) would represent between 0.1 and 0.4% of the muscle composition and between 0.6 and 1.8% of the energy content. More than 80% of the muscle energy content was proteins, and changes in muscle energy content essentially reflected changes in protein content, higher muscle energy content being associated with higher protein content (Fig. 1). Lipids were largely responsible for the variations in liver composition and energy content (Fig. 2). Specific lipid content of the liver varied between 5 and 70% on a wet-weight basis. Smaller variations in protein and glycogen content were observed, protein content varying between 5 and 15% and glycogen content between 1 and 5%. When the energy content in the liver was low, lipids and proteins contributed an equal proportion to total energy content, but as liver energy content increased the energy reserves associated with lipids rapidly became the major energy source, representing 80–90% of total energy stored in the liver (Fig. 2). The regressions between muscle protein content and liver lipid content with the energy content of their respective tissue demonstrate the highly significant ($P < 0.0001$) relationships that exist between the major constituents of muscle and liver and their respective energy content (Table 1).

Energy reserves were located in the muscle at low specific values of somatic energy content, while the liver became the main energy store as specific somatic energy content increased. The total energy content of muscle and liver should

© 1997 NRC Canada

Table 1. Linear relationship between protein and energy content of the muscle and between lipid and energy content of the liver.

	a	*b*	r^2	*P*	*n*
Muscle					
Protein content vs. energy content	–0.97(±0.42)	3.97(±0.12)	0.92	<0.0001	102
Liver					
Lipid content vs. energy content	–11.65(±0.41)	2.75(±0.02)	0.99	<0.0001	91

Note: Mucle and liver energy content (kJ/g wet weight) represent the independent variables and muscle protein and liver lipid content (% wet weight) the dependent variables. The intercept (*a*) and the slope (*b*) are presented with their standard errors in parentheses. Coefficient of determination (r^2), probability level of significance (*P*), and number of fish (*n*) are also presented for each relationship.

Fig. 3. Relative distribution of proteins and lipids in the muscle and liver of cod for differents levels of somatic energy content. Percentage of proteins and lipids in muscle and liver is calculated as the proportion of the total protein and lipid content of the somatic tissue which is the sum of muscle and liver masses.

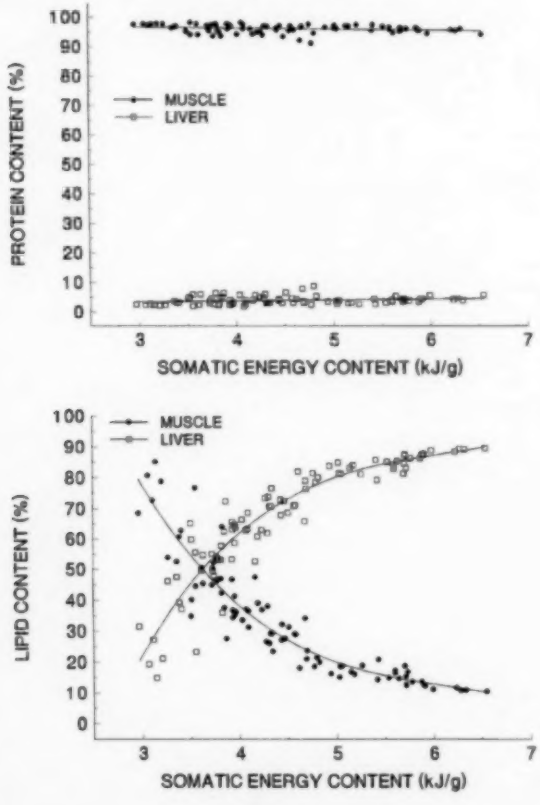
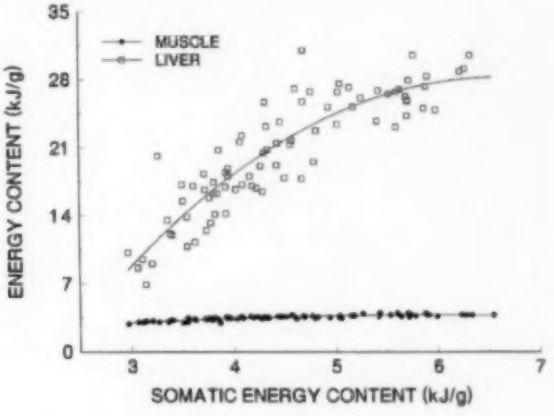


Fig. 4. Changes in the specific energy content of muscle and liver with changes in the specific energy content of the somatic tissue in cod. Specific energy content of the soma is calculated from the total muscle and liver energy contents.



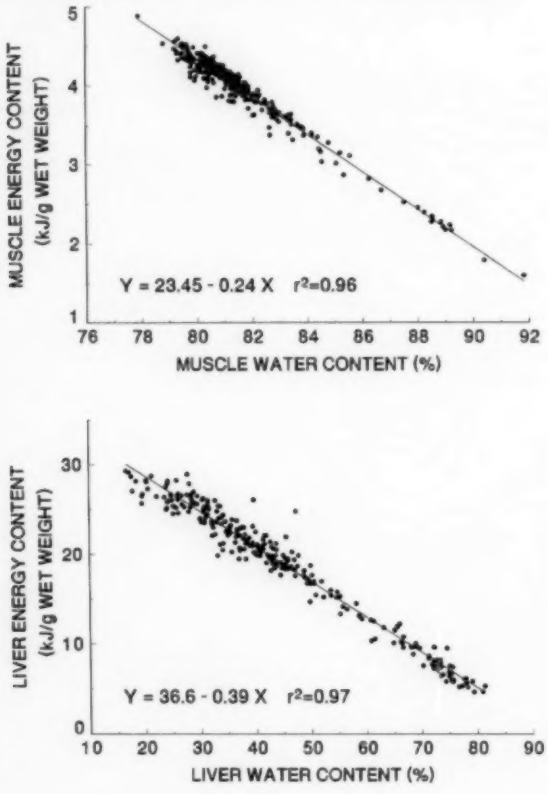
represent the bulk of the energy reserves that cod can mobilize. Their protein, lipid, and energy contents were summed to estimate the somatic protein, lipid, and energy reserves that could be mobilized. More than 90% of the muscle and liver proteins were located in the axial muscle, in both low- and high-energy content situations (Fig. 3). The situation was different for lipids. When fish had low energy reserves, lipid stores were located mainly in muscle and were likely not mobilizable whereas in fish having high energy reserves the bulk of the lipids was located in the liver (Fig. 3). Because the specific lipid content of muscle was constant, the greater relative contribution of muscle lipids to total lipids can be accounted for by changes in the relative weight of muscle and liver and by a decrease in liver lipid concentration in fish with low energy reserves (Fig. 2). Total energy content greatly increased as liver energy content changed, while changes in muscle energy content were not sufficient to have any influence within the range of somatic energy content observed (Fig. 4).

Energy content and condition indices

There was a strong inverse relationship between energy and water content for both muscle and liver tissues (Fig. 5). Muscle energy content ranged from a high value of 5 kJ/g for a water content of 78% to a low value of 1.5 kJ/g for a water content greater than 90%. Liver energy content ranged between 30 (20% water) and 5 kJ/g (80% water). Minimal values were actually observed in moribund cod in the starvation experiment. From such high correlations between specific energy content and water content, very accurate predictions of one component can be made from the measurement of the other.

© 1997 NRC Canada

Fig. 5. Linear relationships between energy content and water content for muscle and liver tissues in cod. Regression equation and coefficient of determination are presented for each relationship.

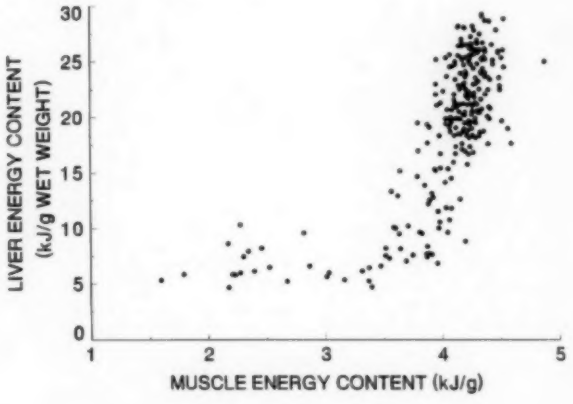

MUSCLE ENERGY CONTENT (kJ/g WET WEIGHT)
Y = 23.45 - 0.24 X r²=0.96
MUSCLE WATER CONTENT (%)
LIVER ENERGY CONTENT (kJ/g WET WEIGHT)
Y = 36.6 - 0.39 X r²=0.97
LIVER WATER CONTENT (%)

The plot of liver and muscle energy content indicates that a large variability in liver energy content was observed at high values of muscle energy content (Fig. 6). Cod with muscle energy content values between 3.5 and 4.5 kJ/g had a widely ranging liver energy content (5 and 30 kJ/g). At lower values of muscle energy content (1.5–3.5 kJ/g), liver energy content was low and constant. The slope of the relationship between liver and muscle energy content was not significant ($P > 0.22$) for values of muscle energy content below 3.5 kJ/g.

Specific muscle and liver energy content increased as condition factor and HSI increased (Fig. 7). The increase in the energetic condition of cod with low condition factor and low HSI was characterized by an increase in both specific energy content of the tissue and tissue masses. This relationship reached a plateau in fish with high condition factor and high HSI values at which point the increases in condition and hence in total energy content were associated with changes in tissue masses and not with changes in specific energy content. Poor condition for cod in the size range of 300–550 mm was associated with condition factor values between 0.4 and 0.6 and HSI values between 0.5 and 1.5%.

Discrete samples of wild cod for which energy content and condition indices were simultaneously determined indicated that the values of total energy content of muscle and liver were also positively related to the condition factor and HSI.

Fig. 6. Plot of liver and muscle energy content for cod sampled between June 1993 and May 1994 in the northern Gulf of St. Lawrence and for cod used in the starvation experiment in 1994.



Total muscle and total liver energy content values of a "standard" 450-mm cod captured at different periods of the year were linearly related to the condition factor and HSI, respectively (Fig. 8). The relationships between total muscle energy content and length and between total liver energy content and length for each period sampled were used to calculate the total muscle and liver energy content of a "standard" 450-mm cod. For each sample, linear regressions between total muscle energy content, total liver energy content, and fork length (log-transformed data) were significant (Table 2).

Condition factor and HSI were independent of size within the size range of cod used in this study (300–550 mm). No significant relationships ($P > 0.05$) were observed between the condition factor, HSI, and length except for sample 4 where the condition factor was negatively related to size ($P < 0.001$). However, a very low slope (−0.0006) and a very low coefficient of determination ($r^2 = 0.18$) were observed. Moreover, the underlying assumption of an isometric growth associated with the use of Fulton's condition factor is respected, as the slopes of the regressions between somatic weight and length for the different samples are all between 2.8 and 3.1.

Discussion

Simple condition indices such as the condition factor and the HSI can clearly be used as indicators of the energy content of cod. Moreover, determination of the water content of muscle and liver provides an accurate means for estimating the energy content of these tissues. These simple measures can be used together to monitor seasonal changes in energy reserves. They can also be used in bioenergetic studies to provide a way of quantifying the energy available to the fish. Consequently, the response of cod populations to variations in environmental conditions could be monitored with these simple indices, as the energy available for the different processes influencing cod productivity will be measurable.

The condition factor and the HSI have been shown to be related to feeding intensity, growth, maturation, fecundity, and survival. Holdway and Beamish (1984) observed that

© 1997 NRC Canada

Fig. 7. Relationship between specific muscle energy content and condition factor and between specific liver energy content and HSI for cod with muscle and liver energy content values covering the full range of energy content for cod. Exponential equations describing the relationships between specific muscle and liver energy content and condition indices are presented.

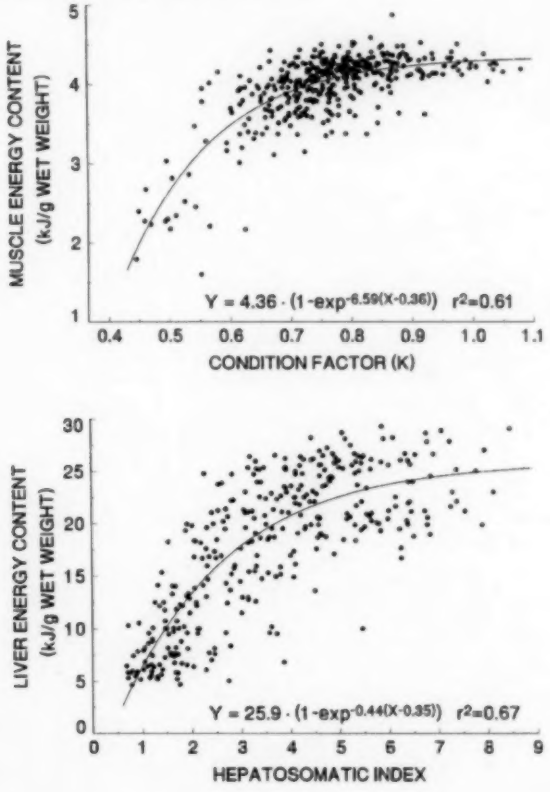
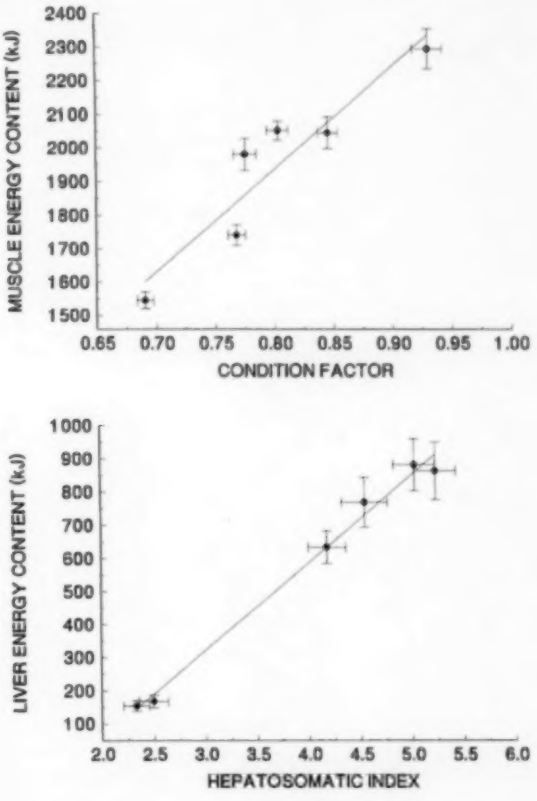

MUSCLE ENERGY CONTENT (kJ/g WET WEIGHT)
Y = 4.36 · (1-exp-6.59(X-0.36)) r2=0.61
CONDITION FACTOR (K)
LIVER ENERGY CONTENT (kJ/g WET WEIGHT)
Y = 25.9 · (1-exp-0.44(X-0.35)) r2=0.67
HEPATOSOMATIC INDEX

Fig. 8. Relationship between total muscle and liver energy content of a 45-cm cod with the corresponding condition factor and HSI for the six samples of cod captured between June 1993 and May 1994 in the northern Gulf of St. Lawrence. Total muscle and liver energy contents were calculated from the linear regressions between muscle and liver energy content with length (log-transformed data) for each sample. Energy contents and condition indices are presented with their standard errors. The number of fish for each sample is between 47 and 76.



specific growth rate in cod was significantly associated with the percentage of lipids in the liver and the HSI. Similar results were obtained by Foster et al. (1993). The condition factor in cod has been assumed to give crude indications of nutritional status and previous nutritional history of fish, cod with a low condition factor presumably resulting from poor feeding conditions (Pedersen and Jobling 1989). Nutritional status and thus condition factor have been demonstrated to influence the fecundity of cod. Actual fecundity in cod was observed to be 20–80% lower than its potential fecundity depending on the nutritional status of the captive fish (Kjesbu et al. 1991). All these results are in agreement with the good correspondence we observed between condition indices (condition factor and HSI), energy content, and biochemical composition. The biochemical composition of cod has been related to its general condition, but in none of the earlier studies have attempts been made to relate clearly defined condition indices to biochemical composition of cod for the whole range of variability in the energy content. For example, very poor condition in cod has been associated with values of muscle water content higher than 84% and with liver lipids lower than 2% (Love 1958, 1960; Black and Love 1986). However, no condition indices were defined. Many studies suggest a good relationship between liver lipids and HSI in cod (Holdway and Beamish 1984; Hemre et al. 1993), but in none of these studies was the relationship defined. In pollock, also a member of the Gadidae, a very good relationship was observed between the biochemical composition of the liver and the liver index (Jensen 1979). The relationships between total muscle and liver energy content and condition indices (condition factor and HSI) for samples of cod captured at different times of the year (Fig. 8) demonstrate the utility of condition indices as tools to follow yearly variations in the energy reserves of cod in natural populations.

The relationships between specific muscle and liver energy content, condition factor, and HSI (Fig. 7) reflect the changes in the biochemical composition of each tissue. Highest muscle and liver energy content values are around 4.5 and 29 kJ/g, respectively (Fig. 7). On a dry-weight basis, these values for muscle and liver energy content would be 22 and 36 kJ/g, respectively. Maximum muscle energy content is close to the

© 1997 NRC Canada

Table 2. Mean values and standard errors for condition factor (K), HSI, and regression parameters describing the relationships between total muscle and liver energy content with length for each sample of cod collected in the northern Gulf of St. Lawrence.

	Sample					
	1 (May 1994)	2 (June 1993)	3 (Jan. 1994)	4 (Oct. 1993)	5 (Sept. 1993)	6 (Aug. 1993)
n	76	56	48	50	48	47
K	0.69 ± 0.007	0.77 ± 0.007	0.78 ± 0.009	0.80 ± 0.008	0.85 ± 0.008	0.93 ± 0.012
HSI	2.33 ± 0.12	2.49 ± 0.14	4.55 ± 0.22	4.18 ± 0.18	5.03 ± 0.20	5.23 ± 0.20
Muscle energy (kJ) vs. length						
a	–4.38	–3.81	–4.53	–3.11	–4.35	–4.32
b	2.85	2.66	2.95	2.42	2.89	2.90
r^2	0.89	0.94	0.91	0.89	0.93	0.92
P	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001
Liver energy (kJ) vs. length						
a	–9.49	–2.48	–5.75	–3.71	–6.26	–5.92
b	4.40	1.77	3.26	2.46	3.47	3.34
r^2	0.35	0.19	0.43	0.24	0.59	0.51
P	<0.0001	<0.003	<0.0001	<0.0003	<0.0001	<0.0001

Note: Regressions used log-transformed data, with values of a and b representing the intercept and the slope, respectively, r^2 the coefficient of determination, P the probability level of significance, and n the number of fish. Fish in each sample were all in the range of 300–550 mm.

energy equivalent of pure proteins (23.6 kJ/g) which represent roughly 90% of the muscle energy composition (Fig. 1), and maximum liver energy content is similar to the energy equivalent of pure lipids (39.5 kJ/g), the corresponding energy composition of the liver being also 90% (Fig. 2). The exponential form of the relationship between specific energy content and condition indices indicates that changes in the condition factor and HSI will be characterized by substantial changes in the weight and specific composition of the muscle and liver at low values of the condition indices followed by an increase in tissue mass and slight further changes in the specific composition at higher values of the condition indices (Fig. 7). Linear relationships between total muscle and liver energy content and the condition factor and HSI demonstrate the influence of tissue mass (total energy content) on the condition factor and HSI (Fig. 8).

The relationships between liver energy content, HSI (Figs. 7 and 8), and the biochemical composition of the liver (Figs. 2 and 3) make the HSI a very good indicator of the total lipid reserves of cod. Lipids are the major constituent of the liver (Fig. 2), and almost all somatic lipids are located in the liver except at low somatic energy content values where most of the lipids are located in the muscle (Fig. 3). Specific lipid content of muscle is constant (Fig. 1). The greater importance of muscle lipids at low somatic energy content (Fig. 3) is therefore the result of the relative importance of muscle mass in association with the decrease in the lipid reserves of the liver at low somatic energy content. However, most of the muscle lipids in cod cannot be considered as lipid reserves, as muscle lipids consist almost essentially of various phospholipids and steryl esters, triacylglycerols, which are used as lipid reserves, representing less than 9% of the total muscle lipids (Jangaard et al. 1967; Lie et al. 1988; Dos Santos et al. 1993). Triacylglycerols, on the other hand, can represent 75–95% of the total liver lipids (Dos Santos et al. 1993). These results are in agreement with other studies stating that cod store lipids almost exclusively in the liver (Holdway and Beamish 1984; Black and Love 1986; Foster et al. 1993). Other species of Gadidae and sharks and rays are also known to store most of their lipids in the liver (Jensen 1979).

The simultaneous use of the condition factor and HSI gives insights into the short- and long-term responses of cod to environmental conditions. Available energy reserves in cod are very compartmentalized, with most of the protein being located in the muscle and most of the lipids in the liver (Fig. 3) (Bogucki and Trzesinski 1949; Dambergs 1964; Jangaard et al. 1967; Eliassen and Vahl 1982*b*; Holdway and Beamish 1984; Jobling 1988; Lie et al. 1988; Kjesbu et al. 1991). Muscle mass can represent 50%–60% of the total weight (Eliassen and Vahl 1982*b*; Houlihan et al. 1988) and thus will have a large influence on the condition factor. On the basis of the relationships between muscle protein content, muscle energy content, and condition factor (Figs. 1, 7, and 8), it is clear that the mobilization of protein will be associated with modifications in the condition factor. On the other hand, modifications in the HSI will reflect mobilization or accumulation of lipids in the liver (Figs. 2, 7, and 8). Black and Love (1986) and Hemre et al. (1993) demonstrated that cod deprived of food used their liver lipids first followed by their muscle proteins. Foster et al. (1993) also observed in a feeding experiment that the HSI responded very rapidly to feeding (35 d). The relationship observed between liver and muscle energy content demonstrates the complementary information that can be obtained by measuring both the condition factor and the HSI (Fig. 6). The large variability in the liver energy content and thus in the HSI for a fairly stable value of muscle energy content (1.5–3.5 kJ/g) (Fig. 5) indicates that the condition factor, which is related to muscle energy and water content, will not respond at the same rate as the HSI to modifications of environmental conditions. For example, differences in HSI between depth strata or between regions for cod with similar

© 1997 NRC Canada

values of the condition factor could indicate differences in short-term feeding intensity between locations.

Fulton's condition factor (K) and the HSI were used as condition indices to describe the condition of cod in this study. The relationships between biochemical composition, energy content, condition factor, and the HSI (Figs. 7 and 8) indicate that the two selected expressions for condition indices are good indicators of the energetic condition of cod.

Fulton's condition factor is one of various formulations used to evaluate the weight–length relationship in fish (reviewed by Bolger and Connolly 1989). The generally accepted assumption is that a heavier weight for a given length corresponds to a better condition. There has been much debate about the best way to express the condition of fish, but none of the expressions used can be considered ideal, each expression having its advantages and disadvantages (Bolger and Connolly 1989; Cone 1989; Springer et al. 1990). Fulton's condition factor was selected because of its simplicity of calculation and because it converts a two-dimensional weight–length relationship into a single statistic that quickly gives a simple indication of the "well-being" of a fish. The major disadvantage of Fulton's condition factor is the assumption of an isometric growth in fish ($b = 3$ in the formula $K = W/L^b$). If this assumption is seriously violated, problems of correlation between condition factor and length could arise. Except for one sample, no significant relationships between condition factor and length were observed in our study for wild cod sampled in the northern Gulf of St. Lawrence. Moreover, the regression coefficients (b) describing the relationship between somatic weight and length ranged between 2.8 and 3.1. These observations justify the use of Fulton's condition factor as an index of condition for cod. However, care should be taken before applying and interpreting the condition factor to cod that have lengths outside the range of 300–550 mm, as this study was limited to that size range. Condition factor was calculated with the somatic weight of cod because energy investment in the gonads is not usually considered part of the energy reserves readily available to the fish, although resorption of gonads in maturing fish that are in poor condition is possible (Kjesbu et al. 1991).

The relative size of the liver can be expressed in different ways. Liver weight has been expressed as a percentage of somatic weight or as a ratio with the cube of body length. Because the relationships between the two forms of the liver index and the liver energy content were comparable, liver weight expressed as a percentage of somatic weight was selected, as it instantaneously provided a clear image of the relative importance of the liver and also because of its independence from body length for the size range studied.

Measurement of the condition factor and the HSI provides a simple and adequate way of estimating the energy reserves of cod. They can easily be used to compare seasonal and annual variations in condition within and between populations. In addition, measurement of the water content of muscle and liver of cod provides an accurate means of estimating the available energy reserves of cod. These indices could advantageously be used to monitor the energetic status of cod stocks and provide a supplementary tool for cod stock management.

Acknowledgements

We thank all who participated in the sampling and dissection of the fish. Special thanks are expressed to Mario Péloquin, Edith Labbé, Louis Fradet, and Isabelle St-Pierre for their technical assistance in fish culture facilities and in the analysis of the biochemical composition and energy content of cod samples.

References

Bagenal, T.B. 1978. Method for assessment of fish production in fresh waters. Blackwell Scientific Publications, London.

Black, D., and Love, R.M. 1986. The sequential mobilisation and restoration of energy reserves in tissues of Atlantic cod during starvation and refeeding. J. Comp. Physiol. B, **156**: 469–479.

Bogucki, M., and Trzesinski, P. 1949. Fluctuations in the water and fat content of the cod. J. Cons. Int. Explor. Mer, **16**: 208–210.

Bolger, T., and Connolly, P.L. 1989. The selection of suitable indices for the measurement and analysis of fish condition. J. Fish Biol. **34**: 171–182.

Cone, R.S. 1989. The need to reconsider the use of condition indices in fishery science. Trans. Am. Fish. Soc. **118**: 510–514.

Costopoulos, C.G., and Fonds, M. 1989. Proximate body composition and energy content of plaice (*Pleuronectes platessa*) in relation to the condition factor. Neth. J. Sea Res. **24**: 45–55.

Dambergs, N. 1964. Extractives of fish muscle. 4. Seasonal variations of fat, water-solubles, protein, and water in cod (*Gadus morhua* L.) fillets. J. Fish. Res. Board Can. **21**: 703–709.

Dos Santos, J., Burkow, I.C., and Jobling, M. 1993. Patterns of growth and lipid deposition in cod (*Gadus morhua* L.) fed natural prey and fish-based feeds. Aquaculture, **110**: 173–189.

Eliassen, J.-E., and Vahl, O. 1982*a*. Seasonal variations in the gonad size and the protein and water content of cod, *Gadus morhua* (L.), muscle from northern Norway. J. Fish. Biol. **20**: 527–533.

Eliassen, J.-E., and Vahl, O. 1982*b*. Seasonal variations in biochemical composition and energy content of liver, gonad and muscle of mature and immature cod, *Gadus morhua* (L.) from Balsfjorden, northern Norway. J. Fish Biol. **20**: 707–716.

Foster, A.R., Houlihan, D.F., and Hall, S.J. 1993. Effects of nutritional regime on correlates of growth rate in juvenile Atlantic cod (*Gadus morhua*): comparison of morphological and biochemical measurements. Can. J. Fish. Aquat. Sci. **50**: 502–512.

Fréchet, A., Gagnon, Y., Schwab, P., D'Amours, D., Dutil, J.-D., Lambert, Y., Bourassa, L., and Rollet, C. 1994. Review of the status of the northern Gulf of St. Lawrence cod stock (3Pn, 4RS) in 1993. DFO Atl. Fish. Res. Doc. 94/29.

Harden Jones, F.R., and Scholes, P. 1974. The effect of low temperature on cod, *Gadus morhua*. J. Cons. Int. Explor. Mer, **35**: 258–271.

Hawkins, A.D., Soofiani, N.M., and Smith, G.W. 1985. Growth and feeding of juvenile cod (*Gadus morhua* L.). J. Cons. Int. Explor. Mer, **42**: 11–32.

Hemre, G.-I., Karlsen, Ø., Lehmann, G., Holm, J.C., and Lie, Ø. 1993. Utilization of protein, fat and glycogen in cod (*Gadus morhua*) during starvation. Fiskeridir. Skr. Ser. Ernær. **6**: 1–9.

Holdway, D.A., and Beamish, F.W.H. 1984. Specific growth rate and proximate body composition of Atlantic cod (*Gadus morhua* L.). J. Exp. Mar. Biol. Ecol. **81**: 147–170.

Houlihan, D.F., Hall, S.J., Gray, C., and Noble, B.S. 1988. Growth rates and protein turnover in Atlantic cod, *Gadus morhua*. Can. J. Fish. Aquat. Sci. **45**: 951–964.

Ironside, J.I.M., and Love, R.M. 1958. Studies on protein denaturation in frozen fish. I — Biological factors influencing the amounts of soluble and insoluble protein present in the muscle of the North Sea cod. J. Sci. Food Agric. **9**: 597–604.

© 1997 NRC Canada

Jangaard, P.M., Brockerhoff, H., Burgher, R.D., and Hoyle, R.J. 1967. Seasonal changes in general condition and lipid content of cod from inshore waters. J. Fish. Res. Board Can. **24**: 607–612.

Jensen, A.J. 1979. Energy content analysis from weight and liver index measurements of immature pollock (*Pollachius virens*). J. Fish. Res. Board Can. **36**: 1207–1213.

Jobling, M. 1988. A review of the physiological and nutritional energetics of cod, *Gadus morhua* L., with particular reference to growth under farmed conditions. Aquaculture, **70**: 1–19.

Jobling, M., Knudsen, R., Pedersen, P.S., and Dos Santos, J. 1991. Effects of dietary composition and energy content on the nutritional energetics of cod, *Gadus morhua*. Aquaculture, **92**: 243–257.

Kjesbu, O.S., Klungsøyr, J., Kryvi, H., Witthames, P.R., and Greer Walker, M. 1991. Fecundity, atresia, and egg size of captive Atlantic cod (*Gadus morhua*) in relation to proximate body composition. Can. J. Fish. Aquat. Sci. **48**: 2333–2343.

Kleiber, M. 1975. The fire of life: an introduction to animal energetics. Krieger Publishing, New York.

Lambert, Y., Dutil, J.-D., and Munro, J. 1994. Effects of intermediate and low salinity conditions on growth rate and food conversion of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **51**: 1569–1576.

Lie, Ø., Lied, E., and Lambertsen, G. 1988. Feed optimization in Atlantic cod (*Gadus morhua*): fat versus protein content in the feed. Aquaculture, **69**: 333–341.

Love, R.M. 1958. Studies on the North Sea cod. III — Effects of starvation. J. Sci. Food Agric. **9**: 617–620.

Love, R.M. 1960. Water content of cod (*Gadus callarias* L.) muscle. Nature (Lond.), **185**: 692.

Love, R.M. 1962. The measurement of 'condition' in North Sea cod. J. Cons. Int. Explor. Mer, **27**: 34–42.

Love, R.M. 1970. The chemical biology of fishes. Academic Press, New York.

Pedersen, T., and Jobling, M. 1989. Growth rates of large, sexually mature cod, *Gadus morhua*, in relation to condition and temperature during an annual cycle. Aquaculture, **81**: 161–168.

Springer, T.A., Murphy, B.R., Gutreuter, S., Anderson, R.O., Miranda, L.E., Jackson, D.C., and Cone, R.C. 1990. Properties of relative weight and other condition indices. Trans. Am. Fish. Soc. **119**: 1048–1058.

© 1997 NRC Canada

Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*)

Martha Krohn, Shannon Reidy, and Stephen Kerr

Abstract: Atlantic cod (*Gadus morhua*) stocks of the Northwest Atlantic have experienced steady decreases in growth rate since 1989 and in physiological condition since 1988. The declines have been attributed to various factors, including size-selective fishing pressure, anomalously low temperature fields, and a decline in available prey. The precise balance of these factors is unknown. We applied simple correlation models to determine that bottom water temperature and capelin (*Mallotus villosus*) biomass together explain 52% of the interannual variance in mean condition of 2J3K cod and 23% of the interannual variance in 2J3KL mean cod growth rates. Bioenergetic models can potentially improve our understanding of the mechanisms behind these relationships because they allocate energy as a function of environmental parameters such as water temperature and prey consumption. We developed a bioenergetic model for Atlantic cod to determine whether temperature could explain the observed decreases in growth rate of northern cod stocks. Our results suggest that the low growth rates of 2J3K northern cod observed in recent years are not due to physiological temperature limitation, while the growth rates of cod inhabiting cooler waters on the northern Grand Banks (3L) may, at least in certain years, be temperature limited.

Résumé : Depuis 1989, les taux de croissance et, depuis 1988, l'état physiologique des stocks de morue franche (*Gadus morhua*) du nord-ouest de l'Atlantique ont diminué. Ces diminutions ont été attribués à divers facteurs, incluant la selection sur la taille par les pêcheries, des températures basses, et une réduction de l'abondance des proies. L'importance relative de ces facteurs est inconnue. Nous avons appliqué des modèles correlatifs pour déterminer que la température des eaux du fond et la biomasse de capelin (*Mallotus villosus*) explique 52% de la variance interannuelle de l'état physiologique de la morue en division 2J3K et 23% de la variance interannuelle du taux de croissance de la morue en 2J3KL. Les modèles bioénergétiques peuvent améliorer notre compréhension de ces relations parce qu'ils divisent l'allocation d'énergie en fonction des variables environnementales comme la température et l'abondance des proies. Nous avons développé un modèle bioénergétique pour la morue atlantique afin de déterminer si la température pouvait expliquer les diminutions des taux de croissance ces dernières années. Nos résultats suggèrent que ces taux de croissance peu élévés en 2J3K ne sont pas limités physiologiquement par la température, mais que ceux de la morue habitant les eaux plus froides en 3L le sont durant certaines années.
[Traduit par la Rédaction]

Introduction

Growth rates of northern cod (*Gadus morhua*) vary greatly among years and have exhibited a pronounced decrease over the last 5 yr on the Labrador and northeast Newfoundland shelves. Although low growth rates have been seen in the past, they are a concern because small size-at-age decreases the overall biomass of the stock and the surplus energy available for reproduction. Cod growth rates also vary spatially, growth rates being lower for cod in colder waters (Taylor 1958; May et al. 1965; Loeng 1989; Brander 1995).

Fish growth rates are influenced by both water temperature, which controls the rate at which food can be assimilated and metabolized, and food supply, which may limit the consumption rates if prey densities are low. The low growth rates of northern cod in recent years may be due to declining water temperatures and/or to changes in capelin (*Mallotus villosus*) biomass or distribution, capelin being the major prey of northern cod (Lilly 1987).

When evaluating the effect of annual variability in ocean temperatures on growth rate, it is important to determine whether varying ocean temperatures do affect the thermal experience of cod. Cod are highly sensitive to slight differences in temperature (less than 0.3°C) and may modify their thermal experience by adjusting their distribution (Rose et al. 1994; Claireaux et al. 1995). We therefore begin the analysis by examining the relationship between temperatures experienced by cod and ocean temperatures on the shelves over the last 12 yr.

To evaluate the importance of temperature and food supply to northern cod growth rates, we examine correlations between temperature, capelin biomass, cod growth, and condition factor in three NAFO divisions (2J, 3K, and 3L) on the Newfoundland and Labrador shelves (Fig.1) over the past 15 yr. Our correlation analysis is an extension of that

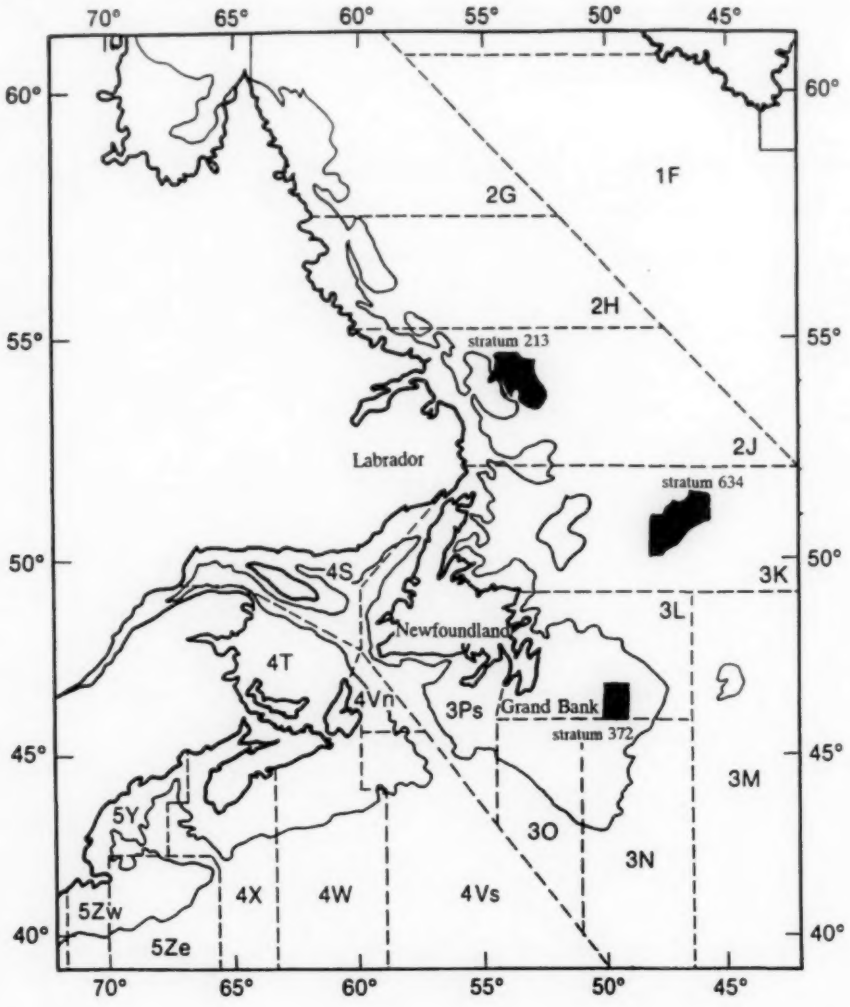
Received March 14, 1995. Accepted February 19, 1996.
J13437

M.M. Krohn,[1] S.P. Reidy,[2] and S.R. Kerr. Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

[1] Author to whom correspondence should be addressed.
[2] Present address: Biology Department, University of Ottawa, Ottawa ON K1N 6N5, Canada.

© 1997 NRC Canada

Fig. 1. Map of the Canadian east coast, locating NAFO divisions 2J, 3K, and 3L and the groundfish survey strata from which the chosen temperatures were taken.



carried out by Bishop and Baird (1993). Although correlations can identify important relationships, they do not identify the mechanisms behind them. Bioenergetic modelling, however, is based on biological mechanism (growth equals energy intake minus energy expenditure) and can help to distinguish between the effects of temperature and prey supply on fish growth.

Kerr (1982) developed a bioenergetic model for Atlantic cod, which we have updated with newly available data on cod physiology. We apply the updated bioenergetic model for Atlantic cod to the northern cod stocks off the coast of Newfoundland and Labrador (NAFO divisions 2J3KL) to assess the potential physiological effects of temperature and food supply on growth. We model potential growth (at maximum prey consumption) using shelf bottom temperatures from 1979 to 1993. We then compare potential and realized growth for cod over this period to determine when and where cod growth rates appear to have been physiologically limited by cold water or by food supply.

Materials and methods

Correlation analysis of temperature and growth

Temperature

The continental shelves off the east coast of Newfoundland and southern Labrador are divided into three NAFO divisions, 2J, 3K, and 3L from north to south (Fig. 1). For the groundfish survey, these divisions are subdivided according to depth contours into 137 strata. Autumn bottom shelf temperatures for the period 1977–1994 were taken from strata 213, 634, and 372 in NAFO divisions 2J, 3K, and 3L (Fig. 1), respectively (Colbourne 1993; E. Colbourne, DFO, St. John's, Nfld., unpublished data). Strata 213 and 634 encompass the area between the 200- and 300-m isobaths just before the shelf break in division 2J and 3K, respectively. Stratum 372 encompasses the

© 1997 NRC Canada

area between the 57- and 92-m isobaths in division 3L. These strata were chosen because they correspond to areas of high cod catches (Lilly 1994).

The temperatures that the cod experience ("cod temperatures") were taken from Rose et al. (1994) and are based on the temperatures at which the cod were trawled during the autumn groundfish survey from 1981 to 1992 and are weighted by catch rates.

Capelin biomass

We used capelin biomass estimates from spring acoustic surveys (Carscadden 1992; Miller 1994, 1995). For divisions 2J and 3K, a continuous time series was not available, so we used an average of Canadian and Soviet estimates for years in which they were both available, and one otherwise. For both the Soviet estimates (1977–1980, 1982–1987, 1990–1991) and Canadian estimates (1981, 1983–1987, 1990–1994) of capelin biomass in divisions 2J and for 3K, we used the combined estimates for 2J and 3K. For the capelin biomass estimates in division 3L, Canadian estimates for 3L specifically were used for the period 1982–1994.

Condition factor

Condition factors ([gutted weight (kg)/length^3 (cm)]·100) were calculated by Bishop and Baird (1993) from weight- and length-at-age from the annual fall groundfish survey. Mean condition factor is a mean of all age-classes for each year from 1977 to 1994 in 2J, 1978 to 1994 in 3K, and 1981 to 1994 in 3L.

Observed growth rates

Observed annual growth rates of northern cod in NAFO divisions 2J3KL were calculated from weight-at-age from the annual fall groundfish survey (Bishop et al. 1995). Growth rate of a given year-class in a given year (i) was determined from the difference in weight-at-age between consecutive years ($W_i - W_{i-1}$). For each year, we chose the year-class weighing closest to 1 kg because that is the size for which the potential growth rates are modelled. In 2J and 3K, 1-kg cod were between 4 and 6 yr old, and in 3L they were between 4 and 5 yr old. Observed growth rates were normalized for a 1-kg fish by dividing growth rates (difference in weight-at-age) by the average of the weight of the fish at the beginning and end of the year ($(W_i - W_{i-1})/[(W_i + W_{i-1})/2]$). Weight-at-age available from the groundfish survey (Bishop et al. 1995) allowed us to calculated growth rates from 1979 to 1993 in 2J3K and from 1981 to 1993 in 3L. Growth rates in 1994 were not included because sample sizes were extremely low from the groundfish survey (Bishop et al. 1995). Growth rates are highly sensitive to small sample sizes because they are inferred from the difference in weight-at-age in two consecutive years whereas condition factors are somewhat less sensitive because they are based on the relationship between length and weight of a single group of fish.

Correction for autocorrelation

A time series cannot be assumed to be a set of independent values because the values are often correlated in time. Therefore the sample size (n) for growth, condition factor, temperature, and capelin biomass time series was corrected for autocorrelation:

$$(1)\quad 1/n^* = 1/n + (2/n^2)\sum_{i=1}^{n}[r(t_i)\cdot(n-i)].$$

The sample size n represents the number of observations (equal to the number of years for which the data were available) and the corrected sample size (n^*) is the reduced sample size to account for the autocorrelation. Autocorrelation at lag i [$r(t_i)$] is the correlation coefficient of the independent and dependent time series at a lag of i years. For multiple regressions, we calculated the autocorrelation of the product of the dependent time series and each of the two independent variables and took the lesser of the two n^*'s.

To correct for lack of independence among divisions, we used the number of observations from only one of two divisions if the dependent variables were correlated. All probabilities associated with the regression statistics were corrected for both autocorrelation and lack of independence among divisions.

Bioenergetic model

Potential growth rates

The bioenergetic model was used to estimate potential growth rates of cod, the rates at which they would grow at the observed temperatures if enough food was available for them to feed at maximum consumption rates. Potential growth, which represents an upper physiological limit to growth, was determined by subtracting the energy costs associated with activity (including standard metabolism), reproduction, heat increment (digestion and assimilation), and waste losses from the energy intake associated with maximum consumption rates, which are temperature dependent. Potential growth from the model (in kilojoules) was converted to weight using an energetic coefficient of 3.95 kJ/g wet weight, an average for cod derived from Edwards et al. (1972) and Daan (1975). Potential growth rates were modelled for cod weighing 1 kg (about 48 cm in length).

Activity metabolism

Activity metabolism was divided into two components, activity associated with feeding and with migration. Kerr (1982) coupled activity metabolism with ration level. We modelled swimming speeds associated with feeding using an experimentally determined relationship from Björnsson (1993) between swimming speeds and consumption rates for cod feeding on live prey in a mesocosm. Because maximum consumption rates are temperature dependent and his experiments were carried out at a higher temperature (8°C), we converted his consumption rates from percentage of maximum ([intake/maximum intake] · 100) to meal size to obtain the following relationship between swimming speed (μ, centimetres per second) and meal size (M, grams wet):

$$(2)\quad \mu = 9.79 + 0.307\cdot M - 0.00131\cdot M^2.$$

Based on maximum consumption rates at the observed temperatures, 48-cm cod swim throughout the day at an average speed ranging from 0.42 to 0.52 bodylengths/s (or 20–25 cm/s). These swimming speeds were converted to metabolic cost using the following relationship between swimming speed (μ, centimetres per second), temperature (T, degrees Celsius), and oxygen consumption (MO_2, micromoles O_2 per hour):

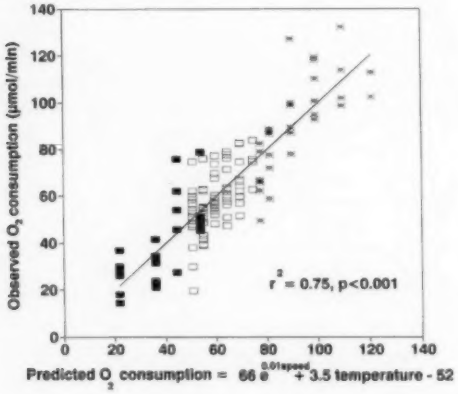
$$(3)\quad MO_2 = 66.5\, e^{0.01\cdot\mu} + 3.48\cdot T - 51.7;\qquad r^2 = 0.75,\ p < 0.001,\ n = 122.$$

We determined this relationship using data from three studies (Nelson et al. 1994; Reidy et al. 1995; Y. Tang, Biology Department, Dalhousie University, Halifax, N.S., personal communication) in which Atlantic cod, weighing from 0.6 to 1.3 kg, were forced to swim in a tunnel respirometer at controlled speeds (10–60 cm/s) over a range of temperatures (2–15°C) (Fig. 2). We normalized the oxygen consumption of each fish to that of a 1-kg fish using a weight exponent of 0.8 (Reidy et al. 1995). Oxygen consumption in this relationship includes oxygen consumed for standard metabolism. Standard metabolism at the different temperatures was estimated by extrapolating the oxygen consumption – swimming speed relationship (equation (3)) to zero (Fry 1971). Oxygen consumption was converted to energy expenditure using the oxycalorific coefficient 13.56 J/mg O_2 (Brett and Groves 1979).

Metabolic costs of forced swimming in a swim tunnel have been shown both theoretically (Webb 1991) and empirically (Boisclair and Tang 1993; Krohn and Boisclair 1994) to underestimate the

© 1997 NRC Canada

Fig. 2. Oxygen consumption of 1-kg cod as a function of swimming speed (cm/s) and temperature (°C). ■, 2°C at 1, 20, 30, and 40 cm/s (Nelson et al. 1994); □, 5°C at 25, 30, 35, 40, 45, and 50 cm/s (Reidy et al. 1995); ∗, 15°C at 15, 20, 30, 40, 50, and 60 cm/s (Y. Tang, unpublished data).



costs of activity in free-swimming fish. Metabolic costs of forced swimming are believed to be less than those of free or spontaneous swimming which has additional costs associated with turning and acceleration. The ratio of spontaneous swimming costs to forced swimming costs (swimming cost ratio, SCR) (excluding standard metabolism) has been found in the above studies to range from 3 to 14, the ratio being smaller for larger fish. Because no data were available for fish as large as 1 kg, we chose a ratio of 1.4, the highest value that would allow for a physiologically realistic potential growth rate; an SCR any higher than 1.4 did not guarantee that potential growth rate remained above the observed growth rate throughout the time series.

To estimate the costs associated with migration, we estimated the annual inshore–offshore cod migration to be approximately 770 km based on routes suggested by Rose (1993). During feeding migrations, cod travel at approximately 20 cm/s (G. Rose, DFO, St. John's, Nfld., unpublished data), suggesting that they spend a total equivalent to 44 d a year swimming across the shelf (or 12% of their time). Metabolic costs associated with this migration velocity and distance were also converted to oxygen consumption using equation (3). We did not multiply by a correction factor (SCR) for swimming costs during migration because we assumed that acceleration and turning costs are negligible for directed swimming associated with migration. Standard metabolism was subtracted because it had already been accounted for in estimating the activity costs associated with feeding. The modelled activity estimates, including standard metabolism and the metabolic costs associated with feeding activity and migration, fell between 2.1 and 3.0 times standard metabolism.

Heat increment

Heat increment (or specific dynamic action), the energy used for digesting and assimilating food, has recently been shown to depend on swimming speed (Blaikie and Kerr 1996). We developed a relationship between swimming speed (μ, centimetres per second) and heat increment (HI, percent energy intake) based on Blaikie and Kerr's (1996) values for heat increment in cod fed capelin swimming at 20, 30, and 40 cm/s in a swim tunnel and Soofiani and Hawkins' (1982) values for heat increment in resting cod fed a diet of fish and invertebrates:

(4) $\mathrm{HI} = 0.0005\,\mu^3 + 11;\ r^2 = 0.91,\ p < 0.0001,\ n = 16.$

We used a heat increment of 13% of energy intake, which was determined by weighting the heat increment according to the frequency distribution of swimming speeds of cod at their lowest activity level (Björnsson 1993). We assumed that cod are not highly mobile while digesting because, although physiologically possible, it is energetically expensive to simultaneously digest food and swim at high speeds. Little direct knowledge, however, is available for the interaction between activity level and digestion in the field. The interaction may well be important; according to equation (4), heat increment rises to 45% for a 50-cm cod swimming at 40 cm/s, a speed at which both feeding (Björnsson 1993) and migrating (G. Rose, unpublished data) cod have been observed to swim. Further investigation into the interaction between digestion, assimilation, and field activity levels would clearly be useful.

Maximum consumption rates

Maximum consumption rates for Atlantic cod were determined using feeding rates from Waiwood et al. (1991) over a range of 0.8–8°C. They found that the amount of food consumed by a 1-kg cod fed to satiation once daily (C_{max}, grams) can be described as the average meal size (17.5 g) multiplied by the probability of feeding on a given day (P):

(5) $C_{max} = 17.5 \cdot P$

where P depends on temperature. We used a P value from their results at 1 and 4°C to obtain a relationship between C_{max} and temperature (T, degrees Celsius):

(6) $P = 0.075 \cdot T + 0.468.$

Maximum consumption was converted from wet weight to energy equivalents using an energy conversion factor of 4.66 kJ/g for the food of North Sea cod 40–49 cm in length (Daan 1975). Braaten and Gokstad (1980) found that cod fed twice a day could eat, on average, 1.2 times more than cod fed once a day and that consumption did not go up when cod were fed more often than twice a day. We therefore multiplied consumption rates from Waiwood et al. (1991) by 1.2. Estimated maximum consumption rates were, on average across years, 4.8 times standard metabolism, in close agreement with Edwards et al.'s (1972) consumption rates for cod fed to satiation, which were, on average, 5.1 times standard metabolism. We used maximum consumption from Waiwood et al. (1991) rather than from Edwards' et al. (1972) because the temperatures were not controlled in Edwards et al.'s (1972) feeding experiments. Waiwood et al.'s (1991) temperature range (1–4°C) covers 35 of the 46 temperatures observed during the three time series for the three divisions. Maximum consumption was extrapolated for the 11 coldest years.

Egestion and excretion

We have chosen a constant value of 20% of food intake for energetic losses through egestion and excretion, a value typical for piscivorous fish (Ursin 1979; Majkowski and Waiwood 1981; Hewett and Johnson 1992).

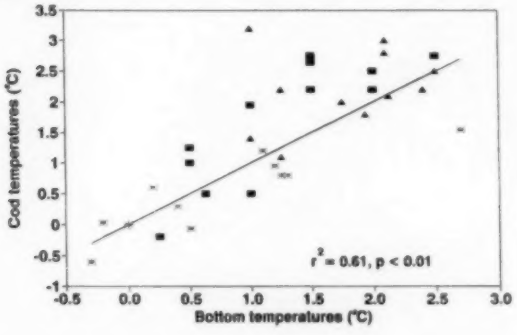
Reproductive losses

The fecundity of a mature 48-cm female cod was calculated using fecundity–length relationships from cod in the appropriate division, 2J3K or 3L (May 1967). The number of eggs (290 000 in 2J3K and 548 000 in 3L) was then multiplied by the energy content of a ripe cod egg, an average of 1.775 J/egg found by Daan (1975) and 2.528 J/egg found by Hislop and Bell (1987). Annual reproductive loss for female cod in 2J3K and 3L was estimated to be 624 and 867 kJ/yr, or 16 and 23% of the energy content of their whole body.

The annual reproductive loss of a mature male cod was calculated from the gonadosomatic index of 5-yr-old male cod (weighing approximately 1 kg) on the Grand Banks of Newfoundland

© 1997 NRC Canada

Fig. 3. Autumn bottom shelf temperature in divisions 2J (■), 3K (▲), and 3L (*) versus temperature for autumn bottom trawled cod (weighted by catch) from 1981 to 1992. The line represents a 1:1 relationship.



(Trippel and Morgan 1994). The cod were believed to be a mix of spent and unspent individuals, so we used the upper limit of the gonadosomatic index (11%) assuming that it would best represent the unspent individuals. The weight of the testes (110 g) was then multiplied by the energy content (3.83 kJ/g wet) of mature ripe male gonad in Pacific cod (*Gadus macrocephalus*) (Smith et al. 1990). The energy content specifically for Atlantic cod testes is not available. Eliassen and Vahl's (1982) energy content for cod gonad (3.49 kJ/g, presumably based on both ovaries and testes) corresponds well to the energy content of the testes of Pacific cod. The annual male reproductive loss was estimated as 383 kJ/yr. Mature male and female reproductive loss was averaged and then multiplied by 50%, the proportion mature at 48 cm in length (Morgan et al. 1993).

Sensitivity analysis

To quantify the effects of parameter uncertainty on potential growth rates, we carried out a sensitivity analysis both by quantifying the effect of the range in the parameters reported in the literature and by varying the parameters systematically by ±10%. The model sensitivity (s) to a change in the parameter was calculated using the following formula:

(7) s = ((modelled growth after perturbation − modelled growth before perturbation) · 100)/modelled growth before perturbation.

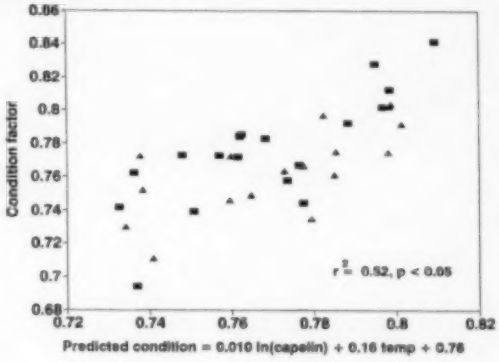
We tabulated the sensitivies for the temperature at which the effect of the perturbation was greatest.

Results

Relationship between autumn shelf bottom temperatures and temperatures for autumn bottom trawled cod

The mean temperatures at which cod were trawled in divisions 2J, 3K, and 3L (T_{cod}, degrees Celsius, "cod temperatures") are significantly related to the autumn bottom shelf temperatures (T_{bottom}, degrees Celsius) in strata 213, 634, and 372, respectively, after correction for autocorrelation (T_{cod} = $1.0T_{bottom}$ + 0.19; r^2 = 0.61, $p < 0.01$) (Fig. 3). The slope is not significantly different from 1, and the intercept is not significantly different from 0, indicating that the shelf temperatures chosen adequately represent the magnitude and interannual variability in the temperatures the cod experience and that cod are found in colder waters in colder years. If the three divisions are considered independently, cod temperatures and bottom shelf temperatures are not significantly correlated in division 3K. The range in temperatures was much smaller in 3K, and there is one anomalous year (1990) when the cod were found above 3°C and the mean bottom shelf temperature was only 1°C.

Fig. 4. Mean condition factor for all age-classes of cod in divisions 2J (■) (1977–1994) and 3K (▲) (1978–1994) (gutted weight/length^3·100) as a function of ln (capelin biomass ('000 000 tons)) and temperature (°C).



For most years, only autumn temperatures were available, although there were seasonal groundfish surveys in 3L in 1985 (spring, summer, autumn, and winter). The average temperature for cod weighted by catch over the four seasons in 1985 was 0.5°C (G. Lilly, DFO, St. John's, Nfld., unpublished data) whereas the temperature we used from the autumn survey alone (stratum 372) was 0.4°C. This difference between annual and autumn temperature (0.1°C) represents less than 3% of the interannual range in 3L autumn bottom shelf temperatures in stratum 372 (−1.0 to 2.7°C). The extent to which autumn and annual temperatures are similar throughout the time series, however, is unknown.

Relationships between capelin biomass, temperature, growth, and condition factor

Temperature and ln (capelin biomass) together explained 52% ($p < 0.05$) of the interannual variability in mean cod condition factor in divisions 2J and 3K (Fig. 4), but were not significantly related to condition factor of 3L cod ($p > 0.05$) (data not shown). Mean annual condition factors of 3L cod were less variable than those in 2J and 3K, ranging from 0.74 to 0.79 in 3L, 0.64 to 0.84 in 2J, and 0.71 to 0.80 in 3K. ln (capelin biomass) alone explained 35% of the variability in 2J3K condition factor ($p < 0.05$).

Temperature and capelin biomass explained 23% of the variability in growth rates ($p < 0.05$) when 2J, 3K, and 3L were included (Fig. 5). Temperature alone explained 56% of the variability in growth rates of 3L cod ($p < 0.01$).

Condition factor and growth rates have both been low in 2J and 3K in recent years. Growth rates have been declining since 1989 or earlier, and condition factors have been declining since 1988 (Fig. 6). Growth rate and condition factor for 1-kg cod, however, were not significantly related over the time series ($p > 0.05$). There is some indication that condition rose in 1994, but there were so few fish caught in the 1994

© 1997 NRC Canada

Fig. 5. Growth rate of 1-kg cod in divisions 2J (■) (1979–1993), 3K (▲) (1979–1993), and 3L (*) (1981–1993) as a function of capelin biomass ('000 000 tons) and temperature (°C).

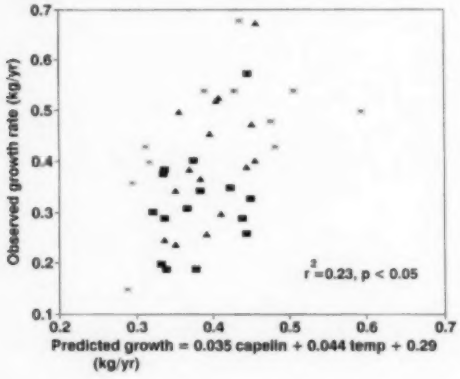
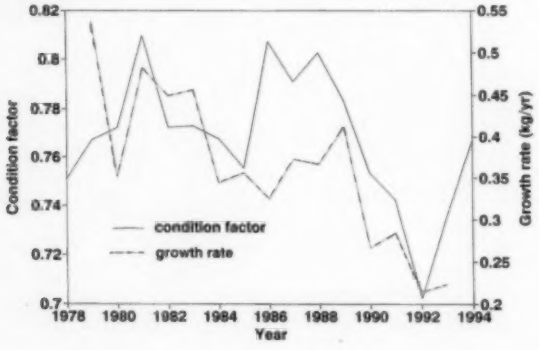


Fig. 6. Mean condition factor for all age-classes of cod in divisions 2J and 3K combined (gutted weight/length^3·100) from 1978 to 1994, and mean annual growth rate of 1-kg cod in divisions 2J and 3K from 1979 to 1993.

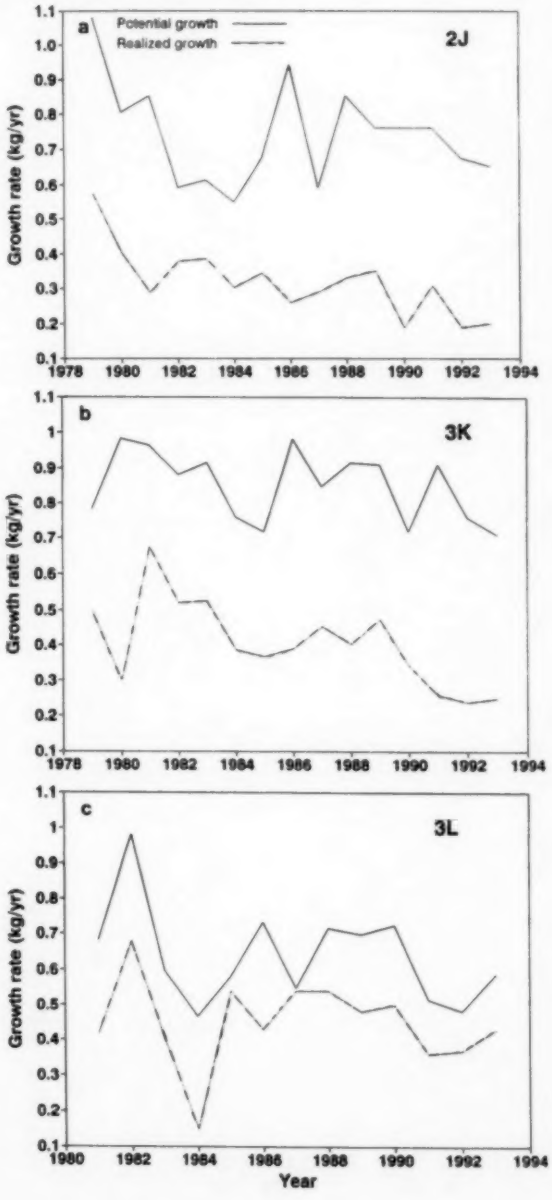


survey that the data must be interpreted cautiously (Bishop et al. 1995).

Potential and realized growth

Realized (or observed) growth falls well below potential growth (generated from the bioenergetic model) in both 2J and 3K (Figs. 7*a* and 7*b*) over the whole time series, from 1979 to 1993. Realized growth reaches, on average, 44 and 48% of potential growth in 2J and 3K, respectively. Differences in potential growth among years and divisions depend entirely on temperature inputs to the model, and the temperature signals that we used for 2J and 3K (from strata 213 and 634, respectively) do not reflect as strong a decreasing trend as do the temperature signals from some other strata. We therefore ran the model with the lowest observed temperatures across the shelf (Colbourne 1993) to obtain a lower limit for the potential growth rates. Since 1986 in 2J, and since 1988 in 3K, realized growth has not reached even these lower limits of potential growth. In 3L, however, realized growth closely follows potential growth over the time series (Fig. 7*c*), realized growth reaching, on average, 70% of potential growth, suggesting that cod in 3L are growing close to the highest rate the temperature regime will allow in most years. Potential growth is lower in 3L than in 2J or 3K, directly reflecting the colder temperatures there. The mean temperatures observed over the available time series are 1.6, 1.8, and 0.7°C for 2J, 3K, and 3L, respectively.

Fig. 7. Potential (modelled) and realized (observed) growth of 1-kg cod in (*a*) division 2J and (*b*) division 3K from 1979 to 1993 and in (*c*) division 3L from 1981 to 1993.



Sensitivity analysis

The effect of a 10% perturbation was most pronounced for parameters associated with activity and consumption (Table

© 1997 NRC Canada

Table 1. Sensitivities of modelled growth to parameter perturbations.

Variable	Value chosen	Literature range	Effect of range (%)	Effect of 10% perturbation (%)
Energy content of whole cod (kJ/g)	3.95	3.85 (Daan 1975) 4.04 (Edwards et al. 1972)	±1	±11
Energy content (kJ/1000 eggs)	2.15	1.775 (Daan 1975) 2.528 (Hislop and Bell 1987)	±3	±2
Fecundity ('000 eggs)	290 548	272–290 (Pinhorn 1984) 403–548 (May 1967)	+2 +6	±2 ±2
Swimming speed (cm/s)	22	10 (Björnsson 1994) 28 (Björnsson 1994)	±235	±27
SCR (spontaneous/forced swim cost)	1.4	1–2 (Boisclair and Tang 1993)	±107	±25
Speed coefficient for O_2 consumption relationship	66.5	53.5 (this study) 79.5	±70	±31
Temperature coefficient for O_2 consumption relationship	3.48	3.25 (this study) 3.71	±4	±7
Constant for O_2 consumption relationship	–51.7	–42.4 (this study) –61.0	±52	±37
Heat increment (% of consumption)	13	10 (Blaikie and Kerr 1996) 13	–28	±12
Energy losses in egestion and excretion (%)	20	16 (Hewett and Johnson 1992) 26	+37 –66	±19
Max. consumption (X standard)	4.8	4.2 (Waiwood et al. 1991) 5.1 (Edwards et al. 1972)	–81 +41	±50
Energy content of diet (kJ/g)	4.66	4 (Daan 1975) 5	–100 +54	±60
Male GSI (% of body weight)	11	6 (Trippel and Morgan 1994) 11	+6	±1
Energy content of testes (kJ/g)	3.83	na	na	±1

1). Perturbations of ±10% resulted in changes in sensitivities of over 25% for swimming speed, SCR, the speed coefficient, and the constant for equation (3) and in sensitivities over 50% for maximum consumption and the energy content of the diet. Parameters associated with reproduction were the most robust with sensitivities of only 1 or 2% for a 10% perturbation.

Sensitivities to the total range of reported values from the literature incorporate both the sensitivity of the model to particular parameters and the degree to which the parameters are known. This analysis also highlights sensitivity of the model to parameters associated with activity and consumption, although the sensitivities of the model to activity parameters from the literature are even higher (70–235%) than the sensitivities to a 10% perturbation because the activity parameters are the least well known and activity costs in the field may be highly variable (Boisclair and Leggett 1989).

Discussion

Our correlation analyses suggest that both temperature and capelin biomass are related to cod condition factor and cod growth rates on the Newfoundland and Labrador shelves. Capelin biomass is most important in the two northerly divisions (2J3K) for condition factor whereas temperature is most

© 1997 NRC Canada

important for growth rates in the colder waters of the most southerly division, 3L. Similarly, our bioenergetic analysis suggests that while food supply may be important in 2J3K, cod growth appears to be temperature limited, at least in certain years, in 3L.

It is pertinent to note that condition factor and growth rates are not correlated and that capelin biomass appears to explain variability in condition factor, while temperature appears to better explain variability in growth rates. We speculate that food supply may be more likely to affect condition because it determines the energy available for gonads and muscle production, while temperature may regulate the development of the whole animal including the growth of the skeleton, i.e., an increase in both length and weight.

The autumn bottom shelf temperatures and "cod temperatures" are calculated from data from the same surveys, with the shelf temperatures being based on temperatures in a single chosen stratum and the "cod temperatures" being based on temperatures in all strata in the division, but weighted by catch. The two sets of temperature data are then not independent, but a strong one-to-one relation between them nevertheless suggests that the temperatures in the strata we chose adequately reflect the temperatures at which the cod were trawled in the greatest numbers and that, throughout the time series, in colder years, cod did not move to warmer areas but did experience colder water.

Despite the recent coincident declines in growth rates, condition factor, and temperature in 2J3K, and despite our finding that cod are not avoiding the cold water, our bioenergetic analysis suggests that the cold water in these two areas has not physiologically limited growth rates. Our bioenergetic analysis has several limitations. Most importantly, variability in temperature over the seasonal cycle is not accounted for. However, a comparison of autumn shelf temperatures and annual temperatures weighted by catch in 3L in 1985 suggests that the autumn bottom shelf temperatures may index the temperature the cod experience throughout the year reasonably well.

We also suffer the common problem of having to make parameter assumptions (Ney 1993), although less so than in the past because of the recent concentrated effort on understanding cod physiology. The sensitivity analysis highlights the model's sensitivity to consumption and activity parameters, and that the sensitivity to activity parameters is exacerbated by the extent to which they are unknown. Further research to constrain the range of swimming speeds, or more importantly costs, would clearly be very useful. Accordingly, the strength of the analysis is in evaluating the differences in the relative importance of food supply and temperature to growth in different areas, and not in the absolute magnitude of the potential growth rates.

The recent low growth rates and condition factors in 2J and 3K northern cod could be because of low prey supply or size-selective fishing pressure, as has been observed in southern Gulf of St. Lawrence cod (Hanson and Chouinard 1992). It is also possible that temperature, even if it has not physiologically limited growth rates, has reduced growth rates indirectly by reducing prey availability. In cold years the cross-sectional area of the cold intermediate layer (CIL) is larger (Colbourne et al. 1994). Cod generally avoid penetrating the CIL, although they may briefly swim up into it in search of capelin, which are generally distributed in colder waters than are cod (Rose and Leggett 1989). In colder years the larger CIL may hamper the cod's ability to prey on capelin, resulting in lower feeding and growth rates. Scatter plots (Shelton and Lilly 1995) and time series (de Cardenas 1994) of CIL and cod growth rates in 2J3KL suggest that in cold years, cod may feed less, even if they are not physiologically limited by their temperature-dependent maximum consumption rates. According to preliminary results (Lilly 1994), cod feeding on capelin was low from 1990 to 1992 in 2J, although the same was not true in 3K.

Unlike cod growth in divisions 2J and 3K, cod growth in 3L does appear, in some years, to be physiologically limited by temperature. Cod in 3L experience colder temperatures than cod in 2J or 3K and are growing, and presumably eating, as much as expected at the temperatures that are available to them. Cod in 3L therefore have lower potential growth rates and need less food to attain them. The absence of a decline in condition factor in cod in 3L compared with cod in 2J3K (Bishop and Baird 1993) could be explained by the possibility that cod in 3L are not food limited.

In summary, our results suggest that cod growth rates are physiologically limited by cold temperatures on the northern Grand Banks, while prey supply and availability are more likely to be limiting growth rates on the northeast Newfoundland and Labrador shelves.

Acknowledgements

We would like to thank Haaken Hop and Daniel Boisclair for useful comments on the manuscript. Funding for this research was provided by an Ocean Production Enhancement Network (OPEN) grant and a Natural Sciences and Engineering Research Council of Canada (NSERC) research grant to S.R. Kerr.

References

Bishop, C.A., and Baird, J.W. 1993. Spatial and temporal variability in condition factors of 2J3KL cod. NAFO SCR Doc. 93/56.

Bishop, C.A., Stansbury, D.E., and Murphy, E.F. 1995. An update of the stock status of Div. 2J3KL cod. DFO Res. Doc. 95/34.

Björnsson, B. 1993. Swimming speed and swimming metabolism of Atlantic cod (*Gadus morhua*) in relation to available food: a laboratory study. Can. J. Fish. Aquat. Sci. **50**: 2542–2551.

Blaikie, H.D., and Kerr, S.R. 1996. Effect of activity level on apparent specific dynamic action in Atlantic cod, *Gadus morhua*. Can.J. Fish. Aquat. Sci. **53**. (In press)

Boisclair, D., and Leggett, W.C. 1989. The importance of activity in bioenergetics models applied to actively predatory fishes. Can. J. Fish. Aquat. Sci. **46**: 1859–1867.

Boisclair, D., and Tang, M. 1993. Empirical analysis of the influence of swimming pattern on the net energetic cost of swimming in fishes. J. Fish Biol. **42**: 169–183.

Braaten, B., and Gokstad, S.L. 1980. Appetite feeding experiments with cod — preliminary results. Int. Counc. Explor. Sea C.M. 1980/f:20.

Brander, K.M. 1995. The effect of temperature on growth of Atlantic cod (*Gadus morhua* L.). ICES Mar. Sci. **52**: 1–10.

Brett, J.R., and Groves, T.D.D. 1979. Physiological energetics. *In* Fish physiology. Vol. VIII. Bioenergetics and growth. *Edited by* W.S. Hoar, D.J. Randall, and J.R. Brett. Academic Press, New York. pp. 279–352.

© 1997 NRC Canada

Carscadden, J. 1992. An overview of capelin in SA2 + Div. 3K and Div. 3L during 1991. CAFSAC Res. Doc. 92/62.

Claireaux, G.Y., Webber, D.M., Kerr, S.R., and Boutilier, R.G. 1995. Physiology and behaviour of free-swimming Atlantic cod (*Gadus morhua*) facing fluctuating temperature conditions. J. Exp. Biol. **198**: 61–69.

Colbourne, E. 1993. Oceanographic conditions during the annual fall groundfish survey in NAFO Divisions 2J3KL. DFO Res.Doc. 93/2.

Colbourne, E., Narayanan, S., and Prinsenberg, S. 1994. Climatic changes and environmental conditions in the Northwest Atlantic, 1970–1993. ICES Mar. Sci. Symp. **198**: 311–322.

Daan, N. 1975. Consumption and production in North Sea cod (*Gadus morhua* L.): an assessment of the ecological status of the stock. Neth. J. Sea Res. **3**: 24–55.

de Cardenas, E. 1994. Some considerations about annual growth rate variations in cod stocks. NAFO SCR Doc. 94/64.

Edwards, R.R.C., Finlayson, D.M., and Steele, J.H. 1972. An experimental study of the oxygen consumption, growth, and metabolism of the cod (*Gadus morhua* L.). J. Exp. Mar. Biol. Ecol. **8**: 299–309.

Eliassen, J.E., and Vahl, O. 1982. Seasonal variations in biochemical composition and energy content of liver, gonad, and muscle of mature and immature cod, (*Gadus morhua* L.) from Balsfjorden, northern Norway. J. Fish Biol. **20**: 707–716.

Fry, F.E.J. 1971. The effect of the environmental factors on the physiology of fish. *In* Fish physiology. Vol. VI. *Edited by* W.S. Hoar, and D.J. Randall. Academic Press, New York. pp. 1–98.

Hanson, J.M., and Chouinard, G.A. 1992. Evidence that size-selective mortality affects growth of Atlantic cod (*Gadus morhua* L.) in the southern Gulf of St. Lawrence. J. Fish Biol. **41**: 31–41.

Hewett, S.W., and Johnson, B.L. 1992. Fish bioenergetics model 2. Univ. Wis. Sea Grant Inst. Tech. Rep. WIS-SG-92-250.

Hislop, J.R.G., and Bell, M.A. 1987. Observations on the size, dry weight and energy content of the eggs of some demersal fish species from British marine waters. J. Fish Biol. **31**: 1–20.

Kerr, S.R. 1982. Estimating the energy budgets of actively predatory fishes. Can. J. Fish. Aquat. Sci. **39**: 371–379.

Krohn, M.M., and Boisclair, D. 1994. Use of a stereo-video system to estimate the energy expenditure of free-swimming fish. Can. J. Fish. Aquat. Sci. **51**: 1119–1127.

Lilly, G.R. 1987. Interactions between Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) off Labrador and eastern Newfoundland: a review. Can. Tech. Rep. Fish. Aquat. Sci. No. 1567.

Lilly, G.R. 1994. Predation by Atlantic cod on capelin on the southern Labrador and Northeast Newfoundland shelves during a period of changing spatial distributions. ICES Mar. Sci. Symp. **198**: 600–611.

Loeng, H. 1989. The influence of temperature on some fish population parameters in the Barents Sea. J. Northwest Atl. Fish. Sci. **9**: 103–113.

Majkowski, J., and Waiwood, K.G. 1981. A procedure for evaluating the food biomass consumed by a fish population. Can J. Fish. Aquat. Sci. **38**: 1199–1208.

May, A.W. 1967. Fecundity of Atlantic cod. J. Fish. Res. Board Can. **24**: 1531–1551.

May, A.W., Pinhorn, A.T., Wells, R., and Fleming, A.M. 1965. Cod growth and temperature in the Newfoundland area. ICNAF Spec. Publ. **6**: 545–555.

Miller, D.S. 1994. Results from an acoustic survey for capelin (*Mallotus villosus*) in NAFO Divisions 2J3KL in the autumn of 1993. DFO Res. Doc. 94/18. pp. 91–98.

Miller, D.S. 1995. Results from an acoustic survey for capelin (*Mallotus villosus*) in NAFO Divisions 2J3KL in the autumn of 1994. DFO Res. Doc. 95/70. pp. 63–71.

Morgan, J.M., Bishop, C.A., and Baird, J.W. 1993. Temporal and spatial variation in age and length at maturity in 2J3KL cod. NAFO SCR Doc. 93/57.

Nelson, J.A., Tang, Y., and Boutilier, R.G. 1994. Differences in exercise physiology between two Atlantic cod (*Gadus morhua*) populations from different environments. Physiol. Zool. **67**: 330–354.

Ney, J.J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. Trans. Am. Fish. Soc. **122**: 736–748.

Pinhorn, A.T. 1984. Temporal and spatial variation in fecundity of Atlantic cod (*Gadus morhua*) in Newfoundland waters. J. Northwest Atl. Sci. **5**: 161–170.

Reidy, S.P., Nelson, J.A., Tang, Y., and Kerr, S.R. 1995. Post-exhaustion metabolic rate in Atlantic cod (*Gadus morhua*) and its dependence upon the exercise regime employed. J. Fish Biol. **47**: 377–386.

Rose, G.A. 1993. Cod spawning on a migration highway in the north-west Atlantic. Nature (Lond.), **366**: 458–451.

Rose, G.A., and Leggett, W.C. 1989. Interactive effects of geophysically-forced sea temperatures and prey abundance on mesoscale coastal distributions of a marine predator, Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **46**: 1904–1913.

Rose, G.A., Atkinson, B.A., Baird, J.W., Bishop, C.A., and Kulka, D.W. 1994. Atlantic cod distribution changes and thermal variation in Newfoundland waters, 1980–1992. ICES Mar. Sci. Symp. **198**: 542–552.

Shelton, P.A., and Lilly, G.R. 1995. Factors influencing weight-at-age of cod off Newfoundland (NAFO Divisions 2J+3KL). ICES C.M. 1995/P:14.

Smith, R.L., Paul, A.J., and Paul, J.M. 1990. Seasonal changes in energy and the energy cost of spawning in Gulf of Alaska pacific cod. J. Fish Biol. **36**: 307–316.

Soofiani, N.M., and Hawkins, A.D. 1982. Energetic costs at different levels of feeding in juvenile cod, *Gadus morhua* L. J. Fish Biol. **21**: 577–592.

Taylor, C.C. 1958. Cod growth and temperature. J. Cons. Int. Explor. Mer, **23**: 366–370.

Trippel, E.A., and Morgan, M.J. 1994. Age-specific paternal influences on reproductive success of Atlantic cod (*Gadus morhua* L.) of the Grand Banks, Newfoundland. ICES Mar. Sci. Symp. **198**: 414–422.

Ursin, E. 1979. Principles of growth in fishes. Symp. Zool. Soc. Lond. **44**: 63–87.

Waiwood, K.G., Smith, S.J., and Peterson, M.R. 1991. Feeding of Atlantic cod (*Gadus morhua*) at low temperatures. Can. J. Fish. Aquat. Sci. **48**: 824–831.

Webb, P.W. 1991. Composition and mechanics of routine swimming of rainbow trout, *Oncorhynchus mykiss*. Can. J. Fish. Aquat. Sci. **48**: 583–590.

© 1997 NRC Canada

Time course of gametogenesis in Northwest Atlantic cod (*Gadus morhua*)

M.P.M. Burton, R.M. Penney and S. Biddiscombe

Abstract: Atlantic cod (*Gadus morhua*) cod are iteroparous (repeat spawners) with diverse patterns of gamete development. Studies of reproduction of wild cod have sometimes been complicated by the presence of spring and fall spawners. By combining data from wild and captive fish from known locations, the present study clarifies the time course of gametogenesis culminating in spawning. There is evidence that females may have an adolescent phase, pausing in stages of oogenesis more advanced than that of immature juveniles. Data also suggest that both male and female adults can omit a spawning; this interruption, still under study, may be a normal facet of cod reproduction in response to low levels of feeding for individual fish. Spermatogenesis seems subject to delays in its initial phases, with fish showing considerable variation in stages attained. Individual males can achieve a higher gonadosomatic index than females, which is unusual. Both male and female cod show large variations in gonadosomatic index for wild reproductive fish, which must mean large variations in fecundity, and may mean that many fish are not reproducing at full potential.

Résumé : Les morues franches (*Gadus morhua*) sont itéropares (elles frayent de façon répétée) et présentent différents modèles de développement des gamètes. Les études portant sur la reproduction des morues en liberté ont parfois été compliquées par la présence d'individus frayant au printemps et à l'automne. En combinant les données pour les poissons captifs et les poissons en liberté provenant de sites connus, la présente étude éclaircit la chronologie de la gamétogénèse qui culmine en la période de fraye. Il semble que les femelles peuvent passer par une phase adolescente, avec arrêts à des stades de l'ovogénèse plus avancés que chez les autres juvéniles immatures. Les données indiquent également qu'aussi bien les mâles que les femelles adultes peuvent sauter une période de fraye; encore à l'étude, cette interruption pourrait s'avérer un aspect normal de la reproduction de la morue, lié à une baisse de l'alimentation chez les individus. La spermatogénèse semble connaître des ralentissements au cours des phases initiales, et la phase atteinte par les poissons mâles au cours d'une période donnée varie considérablement. Certains individus mâles peuvent présenter un indice gonadosomatique plus élevé que les femelles, ce qui est inhabituel. Chez les morues mâles comme chez les morues femelles, les variations de l'indice gonadosomatique, qui sont importantes pour des poissons se reproduisant en liberté, peuvent indiquer de fortes variations de la fécondité; un grand nombre de poissons ne se reproduisent peut-être pas à leur plein potentiel.
[Traduit par la Rédaction]

Introduction

Although Atlantic cod (*Gadus morhua*) has been an important fish, economically, there are gaps in our understanding of its reproduction, probably because it is too large when adult to be studied easily in captivity. However, interest in aquaculture development has been accompanied by some studies of the reproduction of farmed cod (Kjesbu 1988; Kjesbu and Kryvi 1989) with emphasis on females and the final stages of reproduction in broodstock. Consideration of gametogenesis was included in a growth study (Holdway and Beamish 1985), but results were difficult to apply because size of fish and time of spawning were not specified. An intensive study of cod gametogenesis used cod from around Nova Scotia (Morrison 1990). Morrison's work is difficult to interpret for time course data because the fish studied came from a region where there were both fall and spring spawners. This made it impossible to know the duration of earlier stages of gametogenesis. Ideally, to understand the time course of gametogenes, it would be necessary to know what the normal spawning time was. As captive fish, especially those in aquaculture programs, are usually fed optimally for growth, aspects of their reproduction, e.g., fecundity, might not be typical of wild fish. Also, some captive fish are not necessarily getting an appropriate diet, which could adversely affect their reproduction, just as temperature and light regimes may alter the timing of spawning for captive fish. A comparison of captive and wild cod enables a crosscheck of timing, in the event captivity has accelerated or delayed phases of development.

The work reported here sought to clarify the time course of gametogenesis for cod caught off Newfoundland, using both wild and captive cod. Since some long-lived repeat-spawning (iteroparous) fish do not necessarily spawn every year (Burton 1991*a*, 1994), we looked for signs of spawning omission in wild fish and set up preliminary experiments to test whether low feeding level could cause spawning omission in captive fish. Forms of prereproductive gamete development, sometimes regarded as adolescence, have been reported for some teleosts (Sutterlin and Maclean 1984; Brown and Scott 1991) and the possibility that this might occur was also inves-

Received December 30, 1994. Accepted March 16, 1996.
J13445

M.P.M. Burton, R.M. Penney[1] and S. Biddiscombe. Department of Biology and Ocean Science Centre, Memorial University of Newfoundland, St. John's, NF A1B 3X9, Canada.

© 1997 NRC Canada

tigated. As ovarian wall thickness has been useful (Burton and Idler 1987) in distinguishing nonreproductive adults from immature fish, wall measurements were checked among different categories of fish.

Recently the cod population off Newfoundland has drastically declined, with commercial fishing curtailed by moratorium (July 1992), so that access to wild fish and the few farmed fish has been restricted. Hence, our sample sizes are small, but information collected shows a pattern that is important especially in the context of some of the earlier conflicting reports in the European literature, which suggest (Messiatzeva 1932) or refute (Sivertsen 1935) the idea that adult cod may not spawn every year. We include the results of preliminary feeding experiments and plan to do further work if more fish can be obtained.

Materials and methods

Fish

Wild Atlantic cod were donated from Department of Fisheries and Oceans (DFO) cruises in November, North Atlantic Fisheries Organization (NAFPO) division 3L, and February, NAFO divisions 2J, 3K, and 3L, with most fish from 3L. We were given intact fish in formalin for November, but by February the fish were so scarce that DFO could only let us have the formalin-fixed gonads, with accompanying data (weight, length, gonad weight).

Captive fish were obtained from three sources. (1) Previously lightly fed cod were donated from the stock at the Marine Sciences Research Laboratory (MSRL). These fish had been trapped the previous summer close to the MSRL, at Portugal Cove, NAFO division 3L, and had been lightly fed on capelin while in the large stock tanks. Records of exact feeding level were not available.Ten of these fish were killed in November, their length, weight, and gonad weight noted, and samples of the gonads placed in Bouin's fixative. (2) Previously well-fed cod were donated by the Marine Institute (MI). MI fish had been fed optimally since being caught during the summer in locations along the southern shore of the Avalon Peninsula (southwest part of NAFO division 3L). Records of exact feeding level were not available. Fish were killed at the MI in November, and gonads from the fish were fixed in Bouin's for our use, with information on the fish provided to us (weight, length). (3) Previously well-fed cod were purchased from the SeaForest commercial fish farm and were then used for experiments. The fish had been trapped in locations along the southern shore, NAFO division 3L, prior to the cod moratorium. Fish had been well fed while being held in seapens, but records of exact feeding level were not available. These fish were well adapted to captivity. On transfer to the MSRL the fish were held in 900-L tanks, with running seawater at ambient temperature, and under natural photoperiod. Each fish was weighed and measured (fork length) initially. Each was also tagged using a system that would allow easy identification of individual fish with a colour code. Most fish were tagged with coloured fingerling tags at the anterior base of the first and or second dorsal fin. Some fish had a spaghetti tag attached in the lateral musculature using a tagging gun. About 10–15 fish could be comfortably accommodated and discriminated in a 900-L tank. The fish were from an area not associated with fall spawning; before and during the expected spring spawning season, fish were checked manually to see if there was any sign of sperm or eggs being emitted. An egg collector was also fitted to one of the two tanks during the second spawning season to check the occurrence of natural spawning. Fish were fed individually by hand with preweighed male capelin. Fish were either satiated or food limited. Satiated fish were given all that they would accept twice a week in the summer/fall and once every 1 or 2 wk in the winter. Food-limited fish had reduced amounts of capelin per feeding or reduced frequency of feeding. The cod were weighed and measured at intervals; any fish that died was autopsied, the gonads and liver weighed, and samples fixed in Bouin's.

Histology

After fixation, gonad samples were dehydrated, cleared in xylene, embedded in Paraplast, and sectioned transversely at 7–8 μm. Sections were stained in Ehrlich's haematoxylin and eosin. Gonad status (see section below) and degree of atresia were noted and wall thickness was measured for some of the fish. For the wall thickness, five measurements were made for each fish, using one section, and only measuring in regions where there were no large blood vessels in the wall. The developmental stage of the most advanced oocytes was recorded, and oocyte diameter of the most advanced oocyte class was measured for some fish, measuring only fairly round oocytes with the nucleus cut through, and measuring five oocytes per fish. Staging for oocytes was initially based on the Barr system (Barr 1963) and recorded as follows: (1) Immature — small oocytes with dense basophilic cytoplasm and a few large nucleoli, larger oocytes with dense basophilic cytoplasm and with many nucleoli, disposed around the circumference of the nucleus (perinucleolar). (2) Intermediate — oocytes showing signs of cytoplasmic changes immediately preceding endogenous vitellogenesis; cytoplasm with irregular basophilia equivalent to the Balbiani body stage (Wallace and Selman 1981) or "circumnuclear ring" (Morrison 1990). (3) Endogenous vitellogenesis (Anderson 1968) — oocytes with cortical alveoli ("yolk" vesicles Wallace and Selman 1981). (4) Exogenous vitellogenesis (Anderson 1968) — oocytes with vitellogenin-derived yolk in the cytoplasm. Only fish that develop oocytes to the final stage, exogenous vitellogenesis with eosinophilic yolk, are considered to be reproductive adults. Burton (1994) recorded fish that had been arrested at endogenous vitellogenesis, which indicates that the presence of endogenous vitellogenesis does not necessarily mean that a fish will be reproductive for the next spawning season.

For testes, stages were noted as follows: presence of spermatogenic cysts, and presence or absence of sperm.

Data analysis

Condition factor (CF) and gonadosomatic index (GSI) were calculated as follows: CF = weight × 100/length^3; GSI = gonad weight × 100/total body weight. Wall thickness and oocyte diameter for different life history stages were compared using Student's *t*-test.

Gonad status

The fish were chosen to exclude fall spawners. In the case of wild fish the liklihood of fall spawners being present was diminished by selecting the sample site. For captive fish, time of spawning was confirmed by individual examination of the fish, as described earlier.

Partly on the basis of work on winter flounder (Burton and Idler 1987), we initially assumed, for a spring-spawning population of cod, that if a fall-caught fish of either sex had thin gonadal walls, it had not previously been reproductive. To group fish according to reproductive status, we used size and GSI. That is, we assumed that a fish of around 30 cm length would be more likely to be immature than one of 60 cm length (initially based on the DFO wild fish and SeaForest data). Also, fish with high GSI in the fall and winter should be reproductive adults, i.e., fish that would be developing gonads for the spring spawning; fish with a very low GSI in the fall were more likely to be immature, adolescent, or nonreproductive adults, assuming no fall spawners in the sample.

Results

Wild fish

The wild fish, obtained by four DFO cruises in November and February, comprising a total of 112 fish, lengths 23–69 cm, were subject to initial (DFO and ourselves) and final categori-

© 1997 NRC Canada

Table 1. Ovarian wall thickness and GSI for vitellogenic wild cod caught in February in NAFO divisions 2J, 3K, and 3L.

Fish No.	Length (cm)	GSI	Wall thickness (μm)
M4161	39.0	5.74	99
R7163	43.0	2.50	171
R7181	45.0	4.10	140
M1649	53.0	9.62	126
M4133	59.0	10.12	30
R6979	60.0	7.71	101
R6935	63.0	4.33	93
R6932	63.0	2.92	94
R6927	69.0	6.22	36

zation. Thus, a fish initially categorized as immature or as a reproductive adult could later be reassigned on the basis of histology. Twenty-eight females obtained in November ranged in length from 23 to 49 cm. Of these fish, 16 were initially judged to be immature with five possible adolescents distinguished later. Twelve were judged to be reproductive adults; 10 of these had exogenous yolk deposition beginning or well established. The length range in this sample for fish with yolk deposition was 37.4–49.0 cm. Twenty-six females caught in February ranged in size between 27 and 69 cm. Of these fish, 15 were possible adults based on size and/or GSI, but two of the fish, one small (34.0 cm length) and one large (63.0 cm length) did not have true (exogenous) vitellogenesis (yolk deposition) and were reclassified.

The females judged to be immature were distinguished on the basis of GSI, size, and ovarian histology. The GSI of females judged to be immature (n = 21) ranged from 0.1 to 0.6 for fish from 23.3 to 41.0 cm length in November and February. The ovarian wall thickness of these "immature" fish ranged from 28 to 76 μm (mean 48.3 μm), and the oocyte diameter of the largest oocyte class ranged from 50 to 89 μm. For the 12 reproductive fish caught in November, wall thickness varied from 45 to 172 μm, with five fish <77 μm and the remaining seven >90 μm. In February, nine fish with yolky oocytes had wall thickness from 30 to 171 μm. Larger (older?) fish did not necessarily have thicker ovarian walls (Table 1); possibly, as the ovaries enlarged the walls stretched, which caused thinning. Statistically the wall thickness was significantly greater ($p < 0.02$) for all reproductive females as compared with fish rated immature. The oocyte diameter for fish with exogenous vitellogenesis in November ranged from 244 to 412 μm and in February from 375 to 582 μm. These fish did not show any sign of ovulation.

A third group, "adolescent" fish, was tentatively distinguished amongst the "immature" fish caught in November. These five fish had wall thicknesses of 31–66 μm, which was not significantly different from the other immature fish, and the largest oocyte (perinucleolar stage) diameters ranged from 96 to 114 μm, which was significantly larger than those of the other immature fish ($p < 0.001$).

In addition to these groupings, one female was found (February) that did not fit into any of the three categories. She was large (63 cm length) but had a GSI of 0.95 with no yolky oocytes. The largest size class of oocytes in this fish had reached the cortical alveoli stage of development, with a mean diameter of 227 μm; her ovarian wall had a mean thickness of 98 μm. This fish was tentatively classified as undergoing spawning omission for the year because even if she was a fall spawner, she should have been showing signs of exogenous vitellogenesis by February, based on the time course of gametogenesis already indicated.

Males were more difficult to categorize because the formalin fixation was unsuitable for the testicular detail. Nevertheless, spermatogenic cysts and sperm could be detected histologically so that some fish in active spermatogenesis could be identifed as reproductive adults. Thirty males obtained in November ranged in length from 23 to 46 cm. Based initially on the GSI, two males, of six, obtained early November, were adults. These two fish, 42 and 46 cm in length, had GSIs of 0.95 and 1.09, respectively, as compared with GSI <0.08 for the other four fish which had lengths <39 cm.

Twenty-four males obtained in late November had lengths ranging from 23 to 45.8 cm. The GSI of these fish was very variable. The smallest fish (23 cm length) had a very low GSI, <0.03, and eight fish had GSIs <0.08, four <0.5, three around 1.1–1.3, and the rest (eight) 2.15–4.4 (mean 3.16). The eight fish with the largest category of GSIs ranged in length from 37.8 to 45 cm. The longest fish (45.8 cm) had a GSI of 1.31. The histology of these fish showed some testicular development in the case of the fish with the higher GSI: a fish with a GSI of 3.82 had spermatogenic cysts and some sperm already formed, while fish with GSIs of 1.17, 2.64, and 3.64 had active spermatogenesis, but with no sperm detected.

By February, males were showing increasing divergence in GSI; the GSI varied from <0.3 to 12.5, with the lower values inflated because for this sample, weights were rounded to the nearest gram. Fish with GSIs of 3.82, 5.5, 8.0, and 9.35 all had testes in which sperm formed the major stage present, while a fish with a GSI of 7.61 had some spermatogenesis ongoing with some sperm fully formed. The fish with sperm ranged in length from 40 to 66 cm. Two large fish, 62 and 64 cm in length, had no spermatogenesis ongoing and had very low GSIs: 0.22 in each case. These were probably undergoing spawning omission for the year, as even if they were fall spawners, they should have been initiating spermatogenesis by February, based on the time course of gamete formation already indicated.

The GSI of reproductive males, even those with many sperm, showed considerable variation, being as high as 12.5 and as low as 3.8 in February, with a mean of 6.5 (n = 14). Wild females with ovarian exogenous vitellogenesis (advanced yolky oocytes) also showed considerable variation in GSI in February; values ranged from 10.1 to 2.5, with a mean of 5.9 (n = 9). The CFs of the wild fish varied from 0.74 to 1.05 for adult females in November, with males showing a similar range. In February, CFs for reproductive females varied from 0.77 to 0.91, with males showing a similar range.

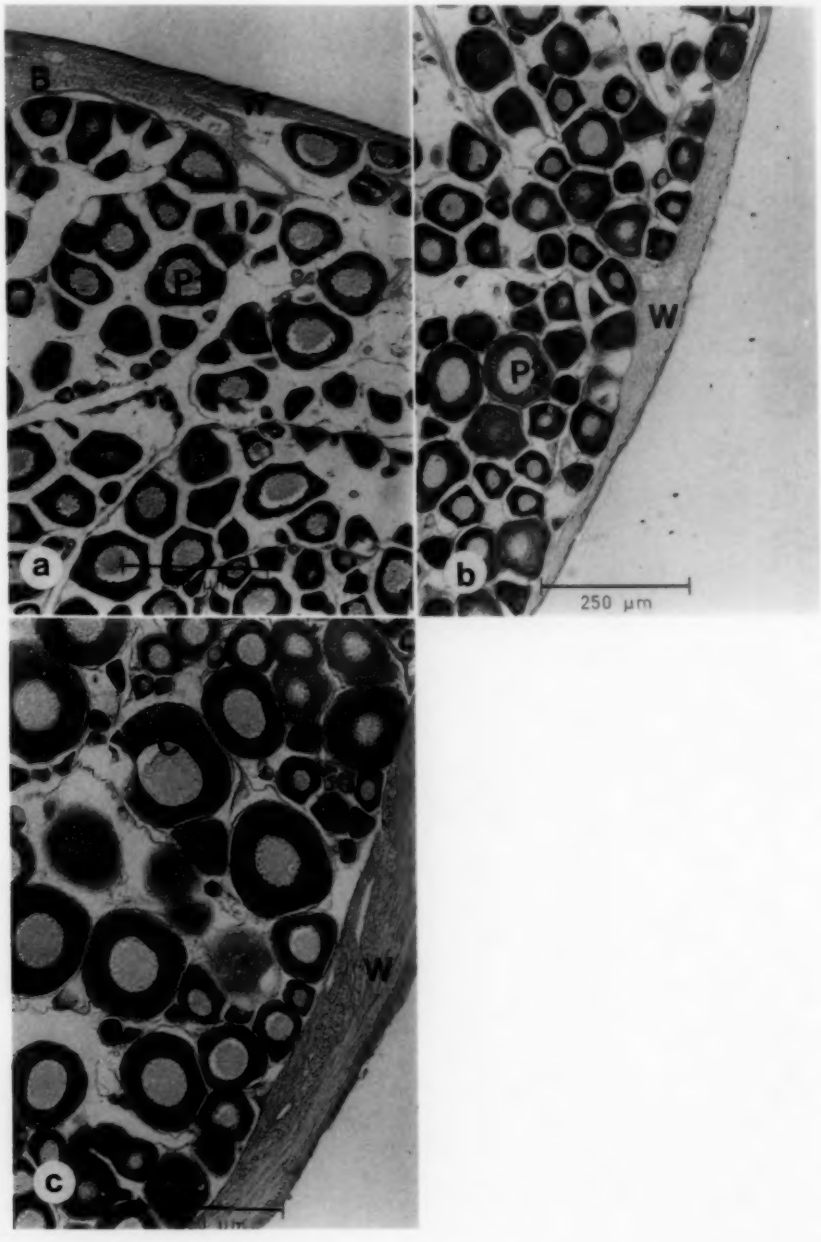
Captive fish

(1) Lightly fed fish. These fish, killed in November, varied in length from 44.0 to 59.0 cm. Six were males and four were females.

None of the four females showed vitellogenesis; three were judged to be immature or adolescent (Figs. 1*a* and 1*b*). The

© 1997 NRC Canada

Fig. 1. Transverse sections of cod ovaries, lightly fed fish, November. (*a*) Fish No. 2: immature/adolescent; thin ovarian wall; most advanced oocytes perinucleolar; early Balbiani bodies. (*b*) Fish No. 1: immature/adolescent; thin ovarian wall; most advanced oocytes perinucleolar plus Balbiani bodies. (*c*) Fish No. 10: nonreproductive adult; thick ovarian wall; most advanced oocytes with cortical alveoli. All figures at same magnification. B, blood vessel; C, oocyte with cortical alveoli; P, perinucleolar oocyte; P1, early Balbiani stage; P2, Balbiani stage; W, ovarian wall.



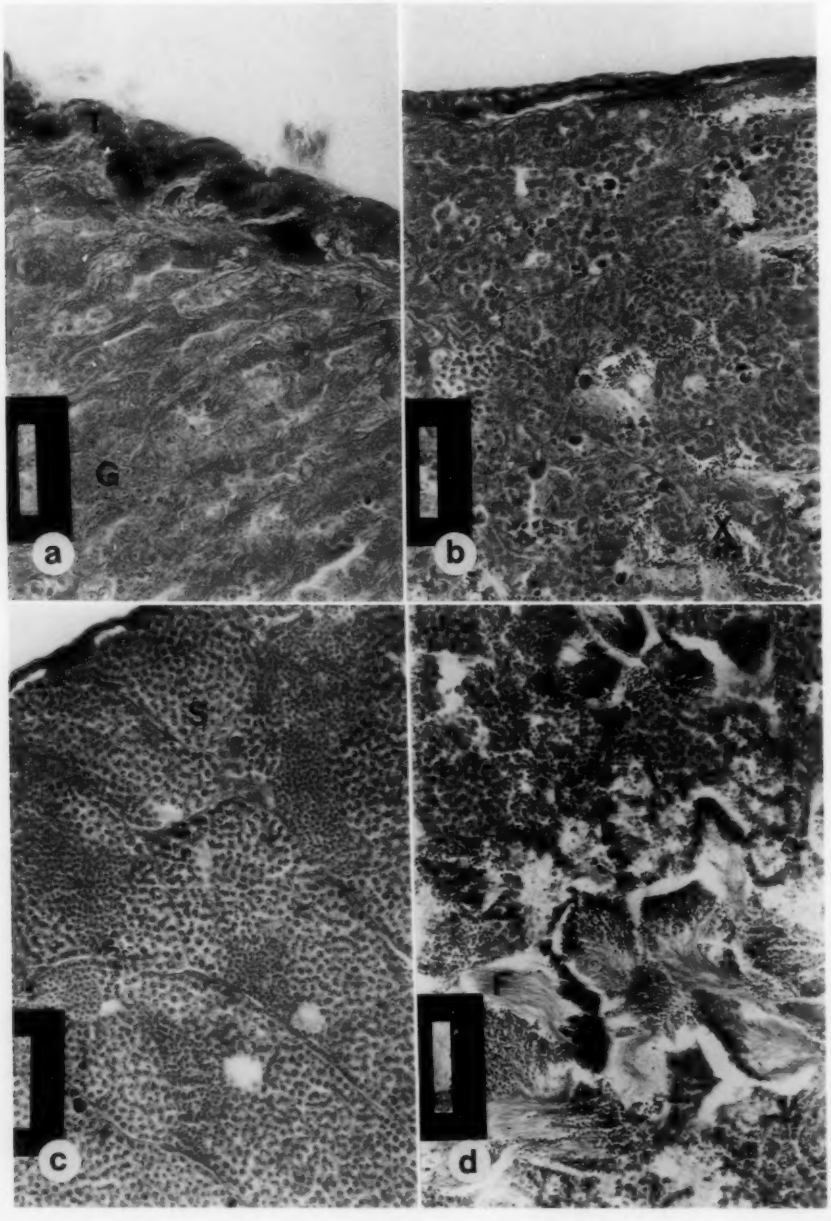
remaining fish had a thick ovarian wall and larger, more advanced oocytes (Fig. 1*c*), but no signs of exogenous vitellogenesis; it was classified as a nonreproductive adult. The CFs of these females were low, 0.59–0.75.

Of the six males, it was concluded that one was a nonreproductive adult; it was large (55 cm length) and had a thick testicular wall (Fig. 2*a*) but no sign of active spermatogenesis. Two were termed delayed because they had early spermatogenesis but no flagellated sperm (Figs. 2*b* and 2*c*). One of the fish (No. 9) may have been undergoing some resorption (Table 2; Fig. 2*b*). The other three fish were in active spermatogenesis with some sperm already formed (Fig. 2*d*). The CFs of these fish were low (Table 2).

(2) MI fish. These well-fed adult-size fish, killed in mid-

© 1997 NRC Canada

Fig. 2. Transverse sections of cod testes, lightly fed fish, November. (*a*) Fish No. 5 nonreproductive adult; thick wall; spermatogonia but few cysts. (*b*) Fish No. 9: delayed, may be resorbing; some cysts, no flagellated sperm. (*c*) Fish No. 4: delayed; many cysts, no flagellated sperm. (*d*) Fish No. 8: reproductive; cysts and flagellated sperm. All figures at same magnification; vertical bar (inner) = 70 μm. F, sperm flagella; G, spermatogonia; S, spermatogenic cyst; T, testicular wall; X, possible spermatids or partially resorbed sperm.



November, lengths 49.1–58.6 cm, had a range of gonad development, with some females showing vitellogenesis macroscopically (yellowish ovaries). The GSIs of the reproductive females was 1.1–4.4, macroscopically identifiable at GSI >3.0. The males had a much greater range of GSIs, 1.2–12.4. CFs of these fish were 0.67–1.30 (n = 15), and the mean of 1.02 was considerably inflated as compared with wild fish and lightly fed MSRL fish.

(3) Experimental fish. The spawning time for these fish was precisely determined for two consecutive years. The earliest recorded release of eggs into the water was 5 May for the first year and 27 April for the second. In the second year, eggs

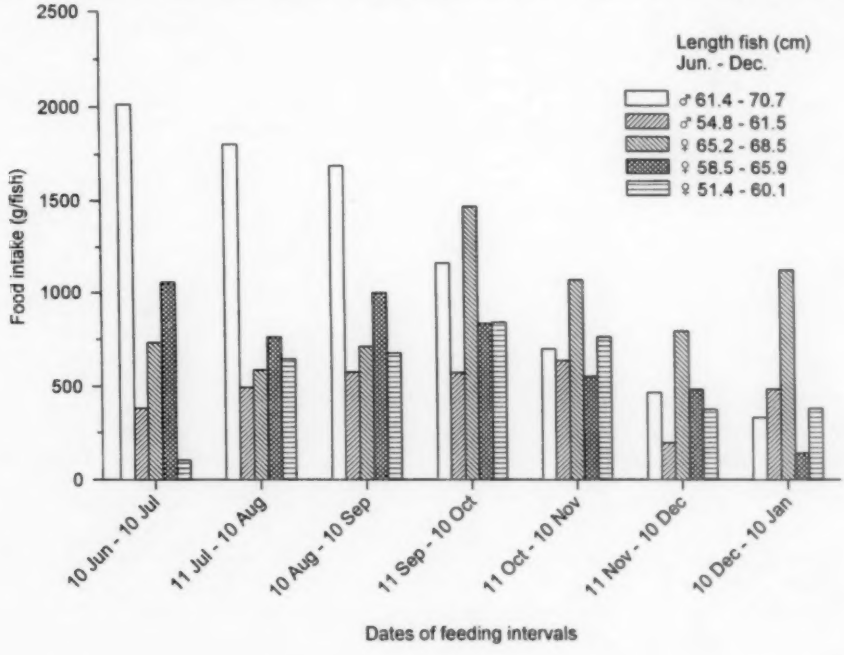
© 1997 NRC Canada

Table 2. Low-condition captive male fish showing variation in reproductive state in November.

Fish No.	Length (cm)	CF	GSI	Histology	Reproductive status
9	44.0	0.61	0.4	Cysts; no flagellated sperm; resorption[a]	Delayed; regressing?
5	55.0	0.51	0.2	Few cysts, no sperm; thick wall	Nonreproductive
4	55.8	0.44	2.5	Cysts, no sperm	Delayed
3	49.5	0.63	1.5	Cysts, sperm	Reproductive
6	50.0	0.77	4.7	Cysts, sperm	Reproductive
8	59.0	0.52	4.7	Cysts, sperm	Reproductive

[a]Some unusual structures looked like the remains of sperm.

Fig. 3. Total food intake, monthly, for individual cod, fed to satiation. The two largest fish, male and female, spawned in early June.



were recorded released into the water until 14 June. Large numbers of eggs were recorded on 21 May and 3 June. On 6 May of the second year, eggs could be expressed from six females and sperm from four males, and on 5 June of the first year, eggs could be expressed from two females and sperm from three males. In the first year, a male that was not spermiating (no sperm could be expressed manually) on 26 March, was spermiating on 28 April. Fertilized eggs were recorded on 14, 17, and 20 May of the second year. In the second year, four dead females autopsied between 15 and 26 June were postspawned, with one showing a few ovulated eggs retained as residual eggs.

Fish individually fed at the MSRL showed considerable variation in their feeding behaviour. When fed to satiation, individuals could take around 10 capelin at any one feeding, but some fish would only take one or two capelin even when other fish were taking much larger amounts. Although there was some variation in size of the fish and larger fish did tend to take larger amounts, the variation was not wholly accounted for by initial size of the fish (Fig. 3). Fish continued to feed in the winter, although intake diminished (Fig. 3). Reproductive females were scarce, but it was possible to track some through the reproductive cycle. Two fish (C016 and P599), which had spawned almost simultaneously in their first captive spawning, were compared with two recently acquired SeaForest (092 and 093) females (Table 3). In late November the lightly fed (since spawning, Table 3), previously reproductive female (C016) had not commenced exogenous vitellogenesis (Fig. 4*a*), while the well-fed SeaForest fish were either immature/adolescent or vitellogenic (Figs. 4*b* and 4*c*), and the well-fed (since spawning, Table 3) captive fish (P599), known to have spawned within a few days of C016, was maturing and spawned the following June.

© 1997 NRC Canada

Table 3. Comparison of four female cod in November, showing a nonreproductive adult as a result of controlled diet and CF.

Fish No.	Length (cm)	Spawning history	Consumption, June–Nov. (capelin, kg (no.))	CF	Reproductive status[a]
C016	62.2	Spawned June	2.21 (66)	0.68	NR
P599	68.5	Spawned June	5.03 (146)	1.07	R
093	63.7	?	Not known	1.11	R
092	46.5	Did not spawn[b]	Not known	0.98	A

[a]NR, nonreproductive, no oocytes in exogenous vitellogenesis; R, reproductive, most advanced oocytes yolky; A, adolescent, thin wall, most advanced oocytes with cortical alveoli.
[b]Based on thin ovarian wall.

Time course of gametogenesis

From the captive fish, it was established that spawning occurred during May and June, and by comparison with the status of gonads found in the other samples, it was concluded that the samples generally were taken from populations with a similar spawning time. Combination of the results gives a time course for spermatogenesis and oogenesis (Fig. 5) for spring-spawning cod off Newfoundland.

Discussion

This study was a product of cooperation in obtaining samples from different sources, although we limited our samples to areas where we expected to have only spring spawners. We saw no evidence of fall spawners in our samples and suggest that variability was therefore due to other factors.

The main aim of this study was to establish the time course of gamete formation for spring-spawning cod off Newfoundland. From the various fish obtained, it is clear that spring-spawning females undergo initial stages leading into vitellogenesis in the late fall, so that GSI is beginning to rise at this time. For fish that normally spawn around May–June, vitellogenesis should be well established by February. Thus, with the time course outlined, a reproductive female expected to spawn in May–June should be showing histological changes by November and macroscopically detectable changes by February, with GSI showing increases between November and February. Changes signifying that a female will be reproductive are detectable approximately 7 mo or more before spawning. This is longer than the 3–5 mo "from the commencement of the ripening process to the moment of spawning" stated by Sorokin (1957), based on Sivertsen's (1935) study. However, Sivertsen was basing his timing on the increase in GSI which may only be detected some weeks after onset of exogenous vitellogenesis. Males in the present study also showed gametogenesis by November, although there was considerable variation in the stages achieved by this time. By February, many fish had testes with fully developed sperm and little evidence of any ongoing spermatogenesis. Overall, therefore, gametogenesis for spring spawners can be detected at least 7 mo before spawning, although males may not be well synchronized at first.

One surprising feature of the GSI in February, for wild fish, was that the mean value for reproductive males could be higher than that for reproductive females. Also for both males and females, there was enormous variation even between fish of very similar length, which presumably means that many fish are not reproducing at their full potential. There was some evidence for the occurrence of an intermediate stage between juvenile/immature and full adult type development. This stage, adolescence, may have been represented by some of the larger "immature" fish which had significantly larger oocytes than the smaller immature fish.

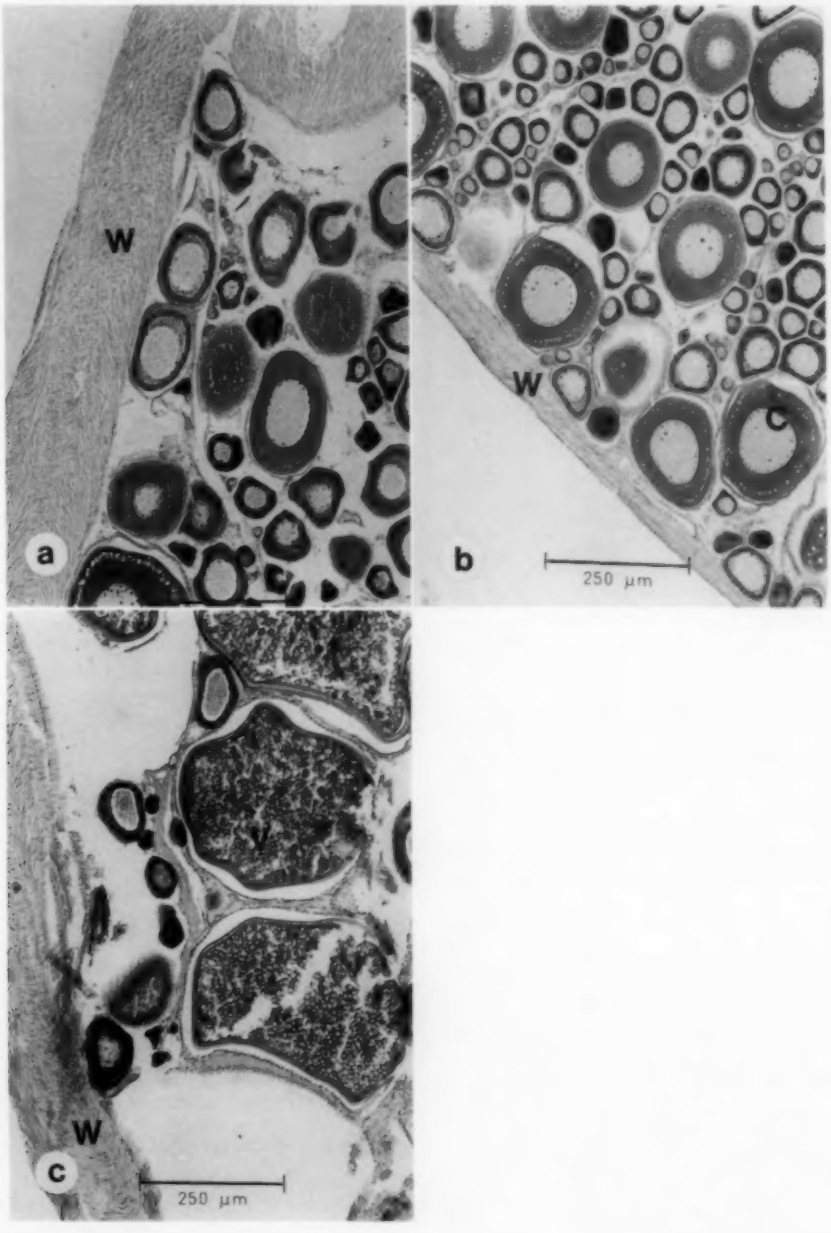
In this study, it was also hoped to learn whether cod would show spawning omission such as has been found for winter flounder (Burton and Idler 1984; Burton 1991*a*, 1994). While the study was ongoing, a report by Oganesyan (1993) relayed information about Barents Sea cod, with tables showing a high proportion of large females, in some areas, with spawning omission, apparently in response to poor feeding. It is not clear from Oganesyan's study exactly what criteria (e.g., GSI, histology, or visual macroscopic inspection) are being applied to distinguish non-reproductive adults.

Oganesyan's (1993) account of spawning omission by cod is not the first such statement from the Russian literature, but it is both more accessible and better documented than some earlier reports, e.g., Messiatzeva (1932) which gives no details but claims that (Barents Sea) cod do not spawn every year,"but approximately only 2 or 3 times in the course of its whole existence". Sivertsen (1935) did not accept Messiatzeva's statement, partly because he saw no such spawning omissions in Baltic Sea cod. Sivertsen suggested that Messiatzeva was confused by including immature fish in the study, but the information in Messiatzeva's paper is not detailed enough to judge the basis for the statements made. Shirokova (1969) also suggested that some Baltic Sea cod did not spawn annually. This suggestion was based on following the course of maturity in cohorts of males and females: the 1956 year class of females showed 99% "maturity" in 1961 but only 89% in 1962, and the 1957 year class of males showed 99% "maturity" in 1961, 87% in 1962, and 92% in 1963.

Gonad wall thickness seems to be a useful tool for separating adults from immature fish, providing that histological examination is possible. Holdway and Beamish (1985) reported that older cod had thicker walls which presents a source of possible confusion if wall thickness is assumed to be only a function of age rather than a product of thickening during the first or subsequent maturations. We found another predictable phenomenon, which is that as ovaries advance into vitellogenesis the ovarian wall may get thinner presum-

© 1997 NRC Canada

Fig. 4. Transverse sections of cod ovaries from laboratory-held or recently obtained farmed fish, November. (*a*) Previously reproductive cod C016: held on a restricted diet from the previous spawning 5 mo earlier; thick ovarian wall; most advanced oocytes with cortical alveoli. (*b*) Cod 092: immature/adolescent; thin ovarian wall; most advanced oocytes with cortical alveoli. (*c*) Cod 093: reproductive adult, and previously reproductive; thick ovarian wall plus most advanced oocytes vitellogenic (exogenous yolk). All figures same magnification as Fig. 1. C, oocyte with cortical alveoli; V, vitellogenic oocyte (exogenous yolk); W, ovarian wall.

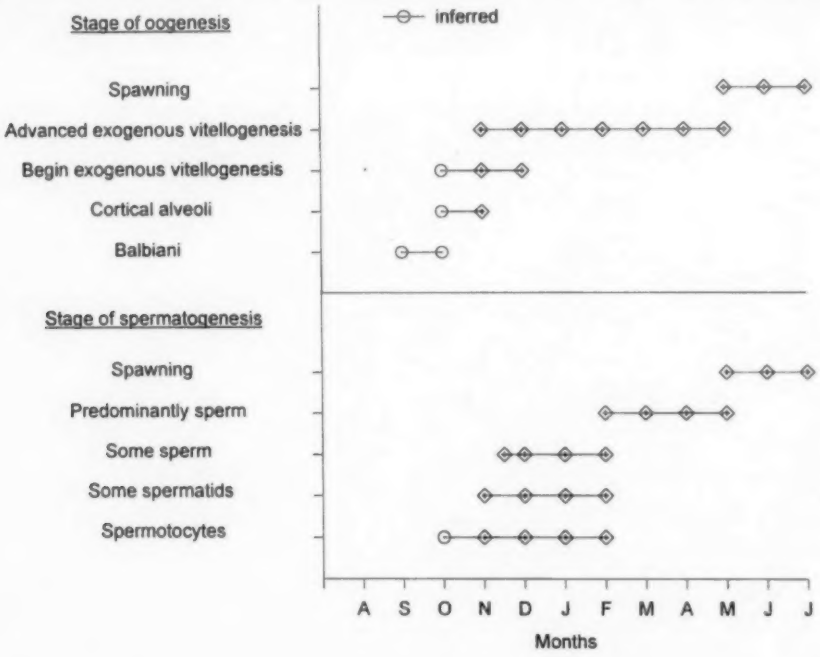


ably due to stretching. This is only of concern if the tissues remain stretched after spawning, but this does not seem to occur. The evidence is consistent that postspawned females have thick ovarian walls, so that postspawned and nonreproductive adults can indeed be differentiated from immature fish that have never spawned.

In studying the time course of gametogenesis for both male and female cod, we have sought to establish a means of separating fish that would spawn in the next season both from immature fish that have never spawned and from any adults that may be totally omitting a reproductive season, a problem emphasized by Shirokova (1977) in discussing Baltic cod.

© 1997 NRC Canada

Fig. 5. Time course of gametogenesis for spring-spawning cod off Newfoundland, based on cod spawning during May and June.



Moreover, by understanding the time taken to reach specific stages, we may be able to separate fish that have a fall-spawning history from the more usual spring-spawning fish. There may be lags in some stages, particularly among the males, some of which seem to start spermatogenesis but then experience delays in completing the final stages. It is not clear whether this is similar to female atresia (absorption of some oocytes), which can reduce fecundity (Horwood et al. 1989), or is the first step towards omission of spawning.

In the current study, only three fish in the wild population, one female and two males, seemed to be nonreproductive adults, assuming that these were not fallspawners with delayed initial stages of gametogenesis. However, the low CFS and highly variable GSIs suggest that many of the wild fish were not functioning optimally and that they may have been experiencing food shortages. Food shortage was correlated with spawning omission in some areas for the Barents Sea cod (Oganesyan 1993), and the relationship was confirmed for North Atlantic winter flounder (Burton and Idler 1984, 1987; Burton 1991*b*, 1994). Further testing this relationship in cod was the basis for examining the effect of restricted diet on captive fish in the present study. Unfortunately, so few cod were available that the results were not definitive. However, one previously reproductive female, which was held on a restricted diet after spawning and which had a low prespawn CF, failed to show exogenous vitellogenesis by late November at a time when other fish from the same source were vitellogenic. Cod are amenable to handfeeding, so if more cod become available, it should be possible to repeat this experiment and obtain detailed information on individual fish. We assume that if cod do omit a spawning that they can subsequently resume reproduction, as occurs for winter flounder (Burton 1991*b*). There is one report in the literature (Wiles 1969) of old females that appeared to have totally ceased reproducing. However, the nonreproductive adult flounder that we obtained from the wild still had reproductive capacity, with immature oocytes present in the ovaries, just as our one experimentally produced nonreproductive cod had many young oocytes. We expect that if spawning omission occurs in wild cod, it follows this pattern, and is not usually terminal except in very old fish. We also predict that specimens would be variable in occurrence, as is the case for winter flounder (Burton 1991*a*) and as reported by Oganesyan (1993) for the Barents Sea cod. The fact that wild cod exhibit large variation in GSI close to spawning may indicate that many of them are close to the threshold of spawning omission for the following year, as well as having low fecundity for the current year. Although cod are supposed to produce millions of eggs per individual, this may be a dangerous assumption, just as it may be unwise to assume that every fish spawns every year after first maturity.

Acknowledgments

We acknowledge financial support from the Dean of Science (Memorial University) and from the Natural Sciences and Engineering Research Council of Canada. Rod Penney was supported by Challenge funding and completed an Honours thesis on cod oogenesis using the wild fish supplied by the Department of Fisheries and Oceans. Lynda Stacey assisted us, as a student in the WISE (Women in Science and Engineering) summer program. The cooperation of personnel in the Marine Institute and the Department of Fisheries and Oceans is gratefully acknowledged. Roy Ficken gave help

© 1997 NRC Canada

and advice on photography. Peter Earle translated works from Norwegian, and Christopher Burton from Russian.

References

Anderson, E. 1968. Cortical alveoli formation and vitellogenesis during oocyte differentiation in the pipefish, *Syngnathus fuscus*, and the killifish, *Fundulus heteroclitus*. J. Morphol. **125**: 23–60.

Barr, W.A. 1963. The endocrine control of the sexual cycle in the plaice, *Pleuronectes platessa* (L.). I. Cyclical changes in the normal ovary. Gen. Comp. Endocrinol. **3**: 197–204.

Brown, E.A.R., and Scott, D.B.C. 1991. Adolescence in the female powan *Coregonus laveratus* (L.) (Salmonidae). Proc. Fourth Int. Symp. Rep. Physiol. Fish Norwich, U.K. 91.

Burton, M.P.M. 1991*a*. A physiological basis for non-annual spawning in winter flounder. Proc. Fourth Int. Symp. Rep. Physiol. Fish Norwich, U.K. 164.

Burton, M.P.M. 1991*b*. Induction and reversal of the non-reproductive state in winter flounder *Pseudopleuronectes americanus* Walbaum by manipulating food availability. J. Fish Biol. **39**: 909–910.

Burton, M.P.M. 1994. A critical period for nutritional control of early gametogenesis in female winter flounder *Pleuronectes americanus* (Pisces, Teleostei). J. Zool. Lond. **233**: 405–415.

Burton, M.P., and Idler, D.R. 1984. The reproductive cycle in winter flounder *Pseudopleuronectes americanus* (Walbaum). Can. J. Zool. **62**: 2563–2567.

Burton, M.P., and Idler, D.R. 1987. An experimental investigation of the nonreproductive postmature state in winter flounder. J. Fish Biol. **30**: 643–650.

Holdway, D.A., and Beamish, F.W.H. 1985. The effect of growth rate, size, and season on oocyte development and maturity of Atlantic cod (*Gadus morhua* L.). J. Exp. Mar. Biol. Ecol. **85**: 3–19.

Horwood, J.W., Greer Walker, M., and Witthames, P. 1989. The effect of feeding levels on the fecundity of plaice (*Pleuronectes platessa*). J. Mar. Biol. Assoc. U.K. **69**: 81–92.

Kjesbu, O.S. 1988. Aspects of the reproduction in cod (*Gadus morhua* L.): oogenesis, fecundity, spawning in captivity and stage of spawning. Dr. Sc. thesis, University of Bergen, Norway.

Kjesbu, O.S., and Kryvi, H. 1989. Oogenesis in cod, *Gadus morhua* L., studied by light and electron microscopy. J. Fish Biol. **34**: 735–746.

Messiatzeva, E. 1932. Chief results of the fishery research in the Barents Sea in 1930 by the GOIN (State Oceanographical Institute of USSR). Rapp. P.–v. Réun. Cons. Perm. Int. Explor. Mer, **81** (Append. 3): 141–151.

Morrison, C.M. 1990. Histology of Atlantic cod, *Gadus morhua*: an atlas. Part 3. Reproductive tract. Can. Spec. Publ. Fish. Aquat. Sci. No. 110.

Oganesyan, M.Y. 1993. Periodicity of the Barents Sea cod reproduction. ICES C.M. 1993 G:64 Demersal Fish Committee.

Shirokova, M.Y. 1969. The sexual maturation rate of the generations of Baltic cod taken from 1961–1963. Tr. Atl. Naucho-Issled. Inst. Rybn. Khoz. Okeanogr. **21**: 37–44. (In Russian)

Shirokova, M.Y. 1977. Peculiarities of the sexual maturation of females of the Baltic cod, *Gadus morhua callarias*. J. Ichthyol. **17**: 574–581.

Sivertsen, E. 1935. The spawning of cod. Fiskeridir. Skr. Ser. Havunders. **4**(10). (In Norwegian)

Sorokin, V.P. 1957. The oogenesis and reproductive cycle of the cod (*Gadus morhua* Linn.). Tr. PINRO, **10**: 125–144. (Transl. by Minist. Fish. Food U.K.)

Sutterlin, A.M., and Maclean, D. 1984. Age at first maturity and the early expression of oocyte recruitment processes in two forms of Atlantic salmon (*Salmo salar*) and their hybrids. Can. J. Fish. Aquat. Sci. **41**: 1139–1149.

Wallace, R.A., and Selman, K. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. **21**: 325–343.

Wiles, M. 1969. Fibrous and cystic lesions in the ovaries of aged Atlantic cod (*Gadus morhua*): a preliminary report. J. Fish. Res. Board Can. **26**: 3242–3246.

© 1997 NRC Canada

Distribution changes and abundance of northern cod (*Gadus morhua*), 1981–1993

D.B. Atkinson, G.A. Rose, E.F. Murphy, and C.A. Bishop

Abstract: Research vessel survey data for cod off Newfoundland (NAFO divisions 2J3KL) were used to examine changes in distribution of the northern cod (*Gadus morhua*) population from 1981 to 1993. The area occupied by northern cod was positively correlated with stock abundance. That is, when more abundant, the stock occupied a larger area, and the observed stock decline was associated with a shrinkage of occupied range. This relationship was demonstrated using two different techniques: area occupied by 90% of the estimated biomass and a statistical ellipse technique describing the bivariate central tendency of the catch data. This latter technique is novel and allows straightforward quantification and visualization of distribution data. The declines in occupied area preceded declines in estimated biomass, confirming previous work which indicated a breakdown in population structure beginning in 1989. The analyses also confirm distribution changes both southward and offshore since 1988. We hypothesize that the cod concentrated in the southern range of the stock beginning in 1990, perhaps as a result of environmental factors, and resultant increases in local density led to increased catchability and fishing mortality for offshore fleets such that catch rates remained high as the stock declined.

Résumé : Nous avons utilisé des données provenant d'études réalisées sur la morue au large de Terre-Neuve (divisions 2J3KL de l'OPANO) afin d'étudier les changements dans la distribution de la population des morues du Nord (*Gadus morhua*) de 1981 à 1993. La zone occupée par la morue du Nord était en corrélation directe avec l'abondance des stocks. Cela signifie que lorsque le stock était plus abondant il occupait une zone plus importante, et que le déclin observé dans les stocks était associé à une contraction du territoire occupé. Nous avons démontré cette relation en utilisant deux techniques différentes : une technique qui visait la mesure de la surface occupée par 90 % de la biomasse estimée et une technique d'ellipse statistique qui permettait de décrire la tendance centrale bivariée des données sur les prises. Cette dernière technique est novatrice et permet la quantification et la visualisation directe des données de distribution. La réduction de la surface du territoire occupé a précédé la baisse de la biomasse estimée, ce qui confirme des études antérieures selon lesquelles une rupture dans la structure de la population aurait eu lieu dès 1989. Les analyses confirment également les changements survenus dans la distribution depuis 1988, soit à la fois un mouvement vers le sud et vers le large. Nous émettons l'hypothèse que, à partir de 1990, la morue du Nord s'est concentrée dans la partie sud du territoire occupé par le stock, peut-être sous l'influence de facteurs environnementaux, et que l'augmentation de la densité locale qui en a résulté a entraîné une vulnérabilité plus grande du stock à la pêche hauturière, et une mortalité par pêche plus élevée dans cette zone, ce qui expliquerait pourquoi les taux de capture sont demeurés élevés alors que le stock était en déclin.
[Traduit par la Rédaction]

Introduction

The cod stock in NAFO divisions 2J, 3K, and 3L ("northern" cod (*Gadus morhua*)) (Fig. 1) has been exploited by inshore gears since the 1500s (Lear and Parsons 1993). Historically, the northern cod stock was the largest cod stock in the Northwest Atlantic, supporting annual inshore catches of >150 000 tonnes (t). With the development of a large offshore fishery by an international otter trawl fleet in the late 1950s, catches gradually increased to a peak of 810 000 t in 1968 (Fig. 2). After that, the stock declined dramatically, and inshore catches rapidly declined to only 35 000 t by 1974 (Fig. 2) (Bishop et al. 1994).

After Canada extended its jurisdiction to 200 miles in 1978, total catches of northern cod gradually increased again and peaked at 267 000 t in 1988, with offshore catches peaking at 179 000 t in 1986 and inshore catches peaking at 113 000 t in 1990 (Fig. 2) (Bishop et al. 1994). Although inshore catches steadily increased through the 1980s, by the mid-1980s the inshore fishers had begun to argue that this cod stock was not increasing at the rate suggested by assessments of the day. The assessment conducted in early 1989 (Anonymous 1989) confirmed that while the stock had been increasing since extension of jurisdiction, the rate of increase was not as great as had been believed.

Problems with the resource continued, such that inshore catches declined to only 60 000 t in 1991 (Bishop et al. 1994). Acoustic research noted a 50% decline in cod migrating shoreward between the springs of 1990 and 1991 (Rose 1993; Bishop et al. 1993). Research vessel survey results (Fig. 3) indicated a significant decline in the trawlable biomass

Received April 6, 1995. Accepted March 11, 1996.
J13436

D.B. Atkinson, G.A. Rose,[1] E.F. Murphy, and C.A. Bishop. Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

[1] Present address: NSERC Chair in Fisheries Conservation, Fisheries and Marine Institute, Memorial University of Newfoundland, St. John's, NF A1C 5R3, Canada.

© 1997 NRC Canada

Fig. 1. Map showing the stock area (NAFO divisions 2J, 3K, and 3L) of northern cod as well as the distribution of fishing stations during a typical annual survey (1987). The 200 mile limit is the boundary of Canadian jurisdiction established in 1977.

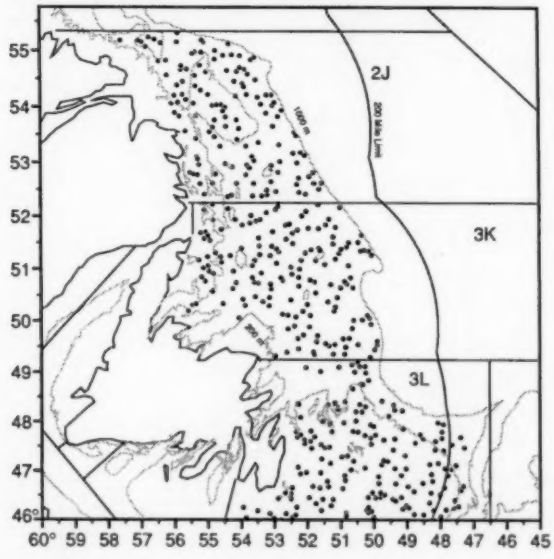
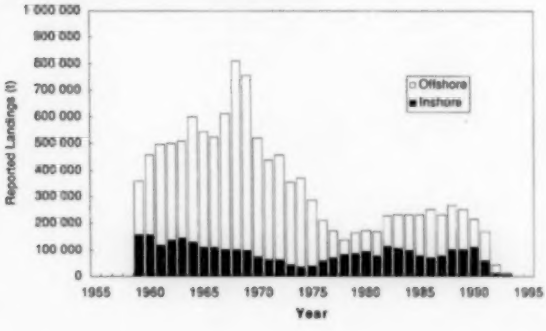


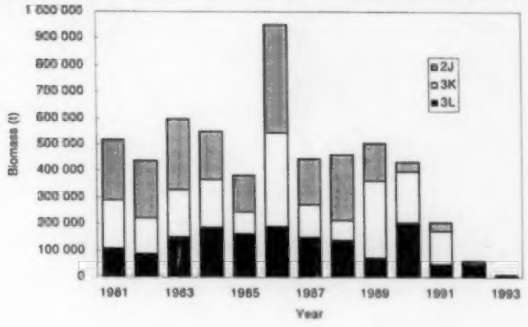
Fig. 2. Annual reported landings of "northern" cod by inshore (fixed gear) and offshore (mobile gear) fleets.



between the autumns of 1990 and 1991. By January and February 1992, the offshore fleet had difficulties finding concentrations of commercial-sized fish. CAFSAC reviewed available data in early 1992 and advised that the stock was at a low level, cautioning that catches should be reduced to the lowest possible level (Anonymous 1992*a*). This evaluation was supported by NAFO in June 1992 (Anonymous 1992*b*). Based on this information, the Minister of the Department of Fisheries and Oceans declared that a moratorium on fishing northern cod would take effect July 2, 1992. The fishery remains closed, and there are presently few indications of stock recovery. Research bottom trawl surveys in autumn and acoustic surveys in spring have both indicated that abundance declines continued in 1993 and 1994 despite the moratorium on fishing in the Canadian zone (Bishop et al. 1994; C.A. Bishop, unpublished data; G.A. Rose, unpublished data).

Changes in distribution in concert with changes in the size

Fig. 3. Annual estimates of trawlable biomass of northern cod in divisions 2J3KL by division from the autumn research surveys.



of the population have been observed for many pelagic species (e.g., Winters and Wheeler 1985). For demersal fishes, the relationship between stock size and range has been examined in relatively few cases, but relationships similar to those demonstrated for pelagic fishes have been observed (Crecco and Overholtz 1990; Rose and Leggett 1991; Swain and Sinclair 1994; Marshall and Frank 1994). Alternative results indicating a poor or weak relationship between stock size and range have also been reported for demersal species (Murawski and Finn 1988; Myers and Stokes 1989).

The dramatic declines in abundance of northern cod have been accompanied by equally dramatic changes in distribution since 1989 (deYoung and Rose 1993). The distribution centroids of the stock, as determined from research vessel and offshore fishery observer data, shifted southward and seaward during this period (Rose et al. 1994). Southerly distribution shifts may have increased the vulnerability of the extant stock to fishing mortality both by Canadian and foreign fleets (Rose et al. 1994). Moreover, fishing catchabilities could have increased if mean local densities remained high or increased as stock area shrank and abundance declined.

To investigate the recent spatial dynamics of the northern cod, we used data from the annual fall bottom trawl surveys to examine changes in overall fall distributions from 1981 to 1993. We put forth two hypotheses: (1) that recent southerly distribution changes would be accompanied by a shrinkage in the range occupied by the stock and (2) that occupied range would be positively correlated with stock abundance. In this paper, we test these hypotheses and then investigate the relationship between stock area and abundance and its potential to provide an index of stock state based on distribution parameters.

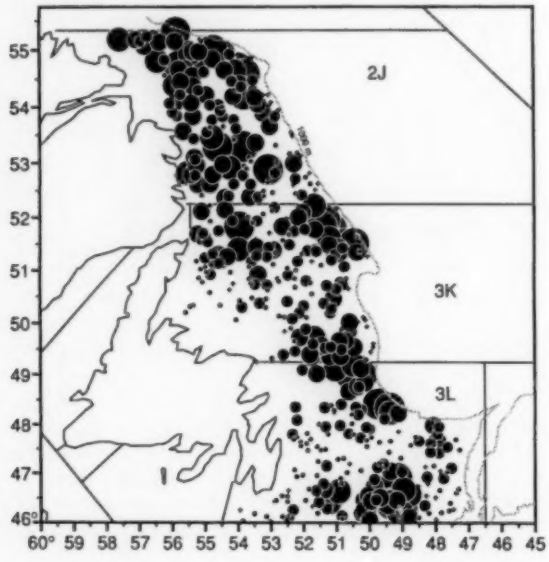
Materials and methods

Annual research bottom trawl surveys to NAFO divisions 2J3KL have been conducted by the Department of Fisheries and Oceans (Canada) beginning in 1981 (Bishop et al. 1994) (Fig. 1). All surveys were conducted during November/early December (with the exception of 1986 when the survey of division 3L was conducted in September) using a stratified-random survey design (Doubleday and Rivard 1981). A total of between 375 and 525 fishing stations were occupied each year using an Engel highrise otter trawl with 29-mm liner in the cod-end. Annual estimates of trawlable biomass by division are obtained using STRAP (Smith and Somerton 1981) (Fig. 3).

It is common practice to examine the distribution of survey

© 1997 NRC Canada

Fig. 4. Example of distribution of cod catches (kg/standard 30-min tow) displayed using an "expanding symbol" plot (1987 autumn survey). Larger circles indicate larger catches.



catches (and changes over time) by visual examination of "expanding symbol" plots (Fig. 4). However, interpretation becomes increasingly difficult with many years of data. Contour ellipses provide a flexible and easily interpreted method of data examination (Warren et al. 1992). Statistical ellipses are centered on the sample means of the X_1 and X_2 variables. The major and minor axes of the ellipses are determined by the unbiased sample standard deviations of X_1 and X_2, and their orientation will result from the covariation between the X_1 and X_2 variables.

Assume that X_1 and X_2 follow a bivariate normal distribution. With covariance matrix S and mean m

$$(1) \quad (X - m)' \cdot S^{-1} \cdot (X - m)$$

is distributed as a chi-square random variable with 2 degrees of freedom. Thus, in order to determine a contour of constant probability p, consider the set of bivariate X's such that equation (1) is less than the value from a chi-square distribution with 2 degrees of freedom at the p probability level.

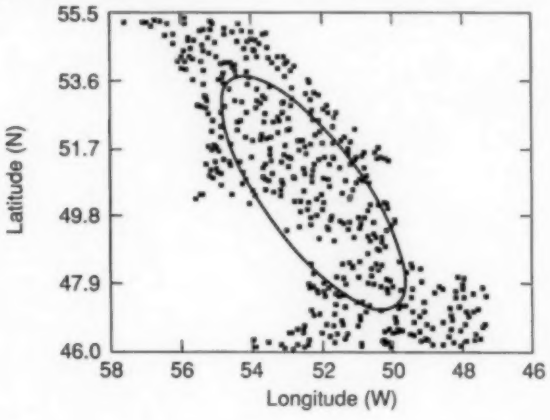
Usually, S and m are unknown, but approximations are available in the form of the sample means and covariance matrixes. Thus, if we take the sample mean, X_{bar} and the sample covariance matrix s, we can consider the set of all point X such that

$$(2) \quad (X - X_{bar})' s^{-1} (X - X_{bar}) \leq p.$$

Ellipses provide information on the central tendency as well as orientation of the data (SYSTAT 1992). It is possible to overlay the results of a number of years of data on a single figure facilitating visual examination.

Discontinuities in fish distribution could cause spurious results (larger ellipse sizes). Hence, we first examined the data visually to ensure continuous distribution. No major discontinuities were found, so the method was applied to the divisions 2J3KL fishing station position (latitude and longitude) data. Each position was weighted by the log transform ($\ln(x)$) of the nonzero cod catch (kilograms) to approximate a bivariate normal distribution. Plots were constructed at the 50% probability level (SYSTAT 1992). This probability was chosen because the resultant ellipses fit within the survey axis boundaries. Probability levels as high as 90% were evaluated in preliminary runs, and all gave similar results.

Fig. 5. Example of a bivariate ellipse (50% probability) determined from the distribution of fishing stations (unweighted by catch) during a typical annual autumn survey of divisions 2J3KL (1987). The ellipse encompasses about 50% of the fishing stations.



We also examined the geographic area of fish distribution using two methods. First, the area contained within each ellipse was determined on a Macintosh PB 7100/66 computer using the public domain NIH image analysis program (developed at the U.S. National Institutes of Health and available from the Internet by anonymous FTP from zippy.nimh.nih.gov or on floppy disk from the National Technical Information Service, Springfield, Va., part No. PB95-500195GEI). Second, the area containing 90% of the estimated biomass was calculated using Delaunay triangles (Watson 1982; Watson and Philip 1985) in ACON (Black 1993). The density contour containing 90% of the biomass was determined through iteration and then the area within that contour determined. The 90% level was judged to be satisfactory based on the reported relationship between abundance and area of distribution of cod in the southern Gulf of St. Lawrence (Swain and Sinclair 1994).

Temperature data are routinely collected from the water column at Station 27 (190 m) off St. John's throughout each year. The depth-integrated annual temperature (seasonal signals removed) at this location has been shown to be a reasonable indicator of conditions in the NAFO divisions 2J3KL area (Petrie et al. 1992).

Results

The unweighted ellipse applied to the position data encircled approximately 50% of the data points as expected (Fig. 5).

Ellipses weighted by the log transform of the weight of the cod catch were very similar and showed relatively little interannual change in the distribution of cod from 1981 to 1987 (Fig. 6*a*). Exceptions occurred in 1984 and 1985 when some southward displacement was evident. Water temperatures were below the decadal average in these years (Fig. 7). After 1987, the ellipses shifted systematically southward and eastward (to deeper water) (Fig. 6*b*). Also after 1987, there was a gradual reduction in the size of the ellipses and the area of distribution. The southward shift and aerial contraction are reflected in the interannual fluctuations in distribution between NAFO divisions (Fig. 3).

© 1997 NRC Canada

Fig. 6. Bivariate ellipses determined from the distribution of cod during the annual autumn surveys of divisions 2J3KL during (*a*) 1981–1987 and (*b*) 1987–1993.

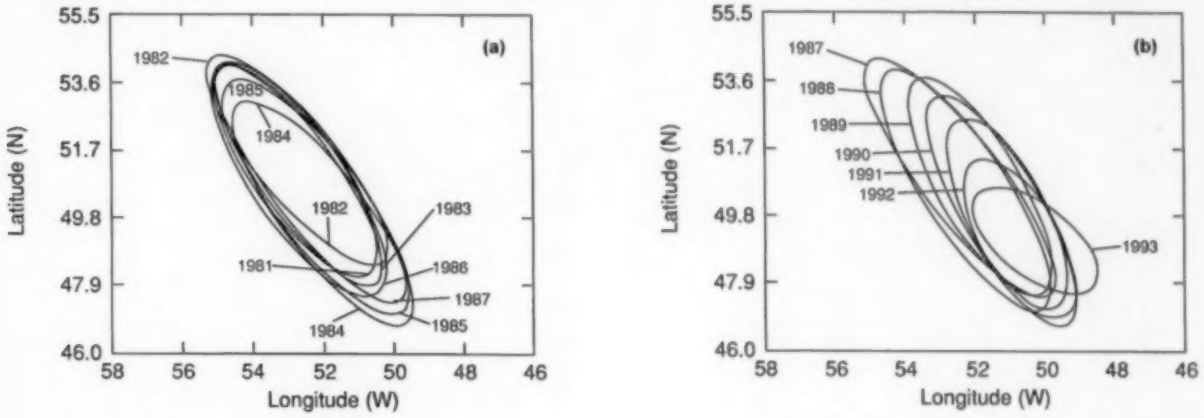


Fig. 7. Depth-integrated annual temperature signal at Station 27 off St. John's, Nfld. (from Rose et al. 1994).

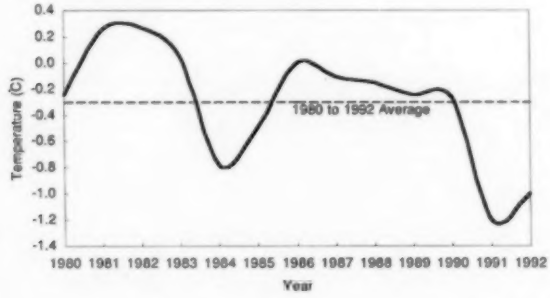
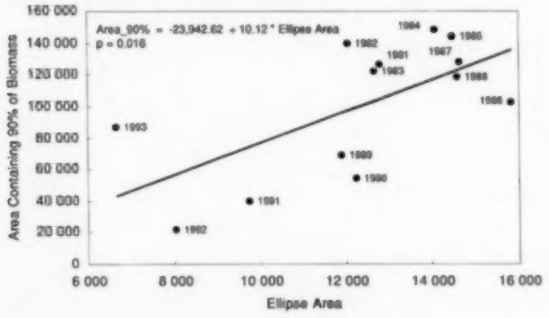
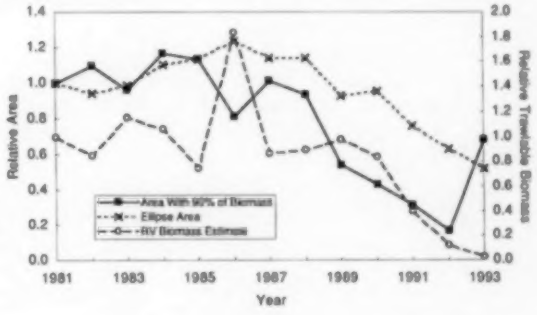


Fig. 8. Regression of ellipse area (square units) on the area containing 90% of trawlable biomass for cod in divisions 2J3KL.



Areas of distribution estimated from the ellipses and from the region containing 90% of the biomass were significantly correlated (adjusted $r^2 = 0.42$; $p = 0.016$) although the fit was not particularly good (Fig. 8). When compared with the trend in estimated trawlable biomass, both measures indicated that a decline in the area of distribution occurred prior to the decline in biomass (area declines began in 1989; stock declines became apparent only in 1991) (Fig. 9). The ellipse series exhibited less variability (SD = 4.21×10^4) than the

Fig. 9. Trawlable biomass from autumn surveys and relative areas of distribution as determined from ellipses and distribution of 90% of trawlable biomass.



biomass series (SD = 2.71×10^3) ($p < 0.001$). Of particular interest is the dramatic increase in the area containing 90% of the trawlable biomass in 1993 (Fig. 8) compared with the continued decline in the area of the ellipses (Fig. 6*a*).

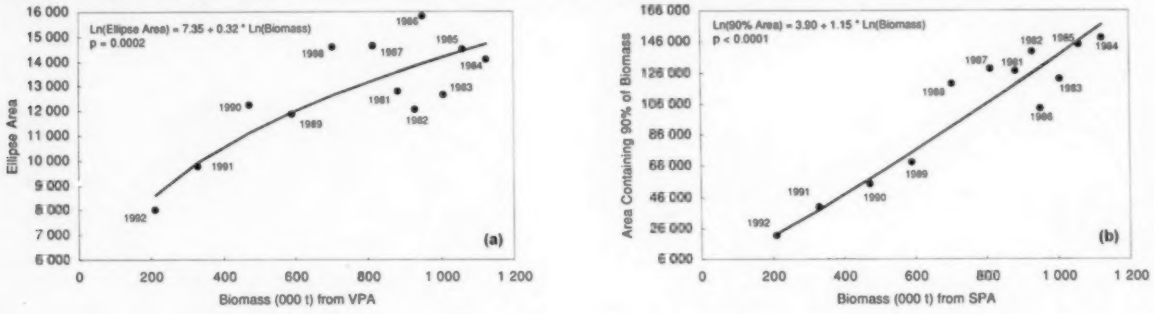
Both the ellipse areas (adjusted $r^2 = 0.73$; $p < 0.01$) and the 90% areas (adjusted $r^2 = 0.95$; $p < 0.01$) were correlated with the biomass of the stock as determined by sequential population analysis (SPA) (Bishop et al. 1993) (Fig. 10).

Discussion

Our data demonstrate that the area cod inhabit from the northern Grand Bank to Labrador (NAFO divisions 2J3KL) is positively correlated with stock abundance. Hence the stock decline that occurred during the late 1980s and early 1990s was characterized by a shrinkage in occupied range. This result is supported by both the statistical ellipse technique describing the central tendencies of the research survey catch data and the area encompassing 90% of the stock biomass as calculated from the same data. Similar results describing stock area–biomass relationships have been reported for many pelagic fishes (see review in Winters and Wheeler 1985) and for a lesser but growing number of demersal fish populations (Crecco and Overholtz 1990; Rose and Leggett

© 1997 NRC Canada

Fig. 10. Regression of (*a*) ellipse area (square units) and (*b*) area containing 90% of research vessel biomass on population biomass as determined from sequential population analysis (SPA) (Bishop et al. 1993). Log transforms were used to standardize variances.


Ln(Ellipse Area) = 7.35 + 0.32 * Ln(Biomass)
p = 0.0002
Ellipse Area
Biomass (000 t) from VPA
(a)
Ln(90% Area) = 3.90 + 1.15 * Ln(Biomass)
p < 0.0001
Area Containing 90% of Biomass
Biomass (000 t) from SPA
(b)

1991; Gordoa and Hightower 1991; Swain and Wade 1993; Swain and Sinclair 1994).

A positive relationship between range and abundance is tenable only for populations exhibiting strong associative behaviour where average local densities (those within aggregations, or within areas occupied by groups of aggregations) remain relatively constant in relation to and over a range of abundance levels (referred to as "hyperstability" by Hilborn and Walters (1992)). Northern cod exhibited hyperstability during their decline. The biomass of northern cod has ranged from levels of the order of millions to tens of thousands of tonnes in the past half century (six orders of magnitude) whereas variations in local densities are almost certain to have been much less. Direct evidence of local density stability comes from the catch rates of mobile gear which remained rather stable, or even increased, from the early 1980s onwards (Baird et al. 1992) and from acoustic densities of spawning and postspawning migrating aggregations which did not decline as did abundance levels in the early 1990s (Rose 1993). This behaviour is thought not to be unique for northern cod. In the northern Gulf of St. Lawrence, average local densities of cod ranged within one order of magnitude whereas the abundance ranged over several during a comparison of year-to-year fish availabilities and fishing success (Rose and Leggett 1991).

We question whether or not our findings would hold year-round for all ages. Our results apply for the most part to cod of ages >3 yr during the fall period of offshore migration to wintering areas. There is evidence that a basic range–abundance relationship holds during the spring and summer periods as well for these older fish (Rose and Leggett 1991; Rose 1993; Bishop et al. 1993). However, we cannot be certain if this or any population size – distribution relationship holds for the less migratory juveniles of ages <3 yr whose distribution patterns are more likely to be related to habitat selection (J. Anderson, Department of Fisheries and Oceans, NAFC, St. John's, Nfld., personal communication).

Could our results be confounded by recent systematic delays in the timing of the migration (Colbourne et al. 1997)? Delays would result in the later data representing an earlier stage in the migration cycle, when cod are likely to be more dispersed. Hence, any bias from that source would be toward a wider dispersion in later years, and not a greater concentration as observed. Also, the central change in distribution was southerly and not cross-shelf. Both these results argue against migration timing changes as key determinants of the correlation between range and biomass observed here.

Our analyses demonstrate similar trends in the distributional measures (90% area and ellipse) from 1981 to 1992, but divergence in 1993. The divergence almost certainly resulted from the lack of any appreciable concentrations of cod being located in 1993 (Bishop et al. 1994) as a result of the small stock size relative to the survey sampling intensity. The ellipse method remains correlated with abundance under this circumstance whereas the 90% area method does not. An additional method, the GINI index, has also been used to demonstrate range decline and concentration in northern cod (Myers and Cadigan 1995).

Marshall and Frank (1994) also reported that tests of range and abundance correlation may depend on the technique used. Indeed, these relationships between range and abundance may be confounded by changing behaviours as cod concentrated to the south. For example, in 1991 and 1992, despite the declining biomass, stock range is *less* than would be expected under the assumption that the relationship between range and biomass holds at very low stock sizes (Fig. 10). Despite such complications, the general patterns of change in distribution properties may be more immediately responsive than abundance to various environmental changes and hence provide an early warning of coming changes in fish abundance states. For example, an early indication of stock rebuilding in northern cod may be an expansion of the distribution to patterns of the mid-1980s (deYoung and Rose 1993; Rose et al. 1994; Taggart et al. 1994).

How general are our results? We believe that they are likely to apply to all cod populations (e.g., Rose and Leggett 1991; Swain and Wade 1993). However, demersal populations are unlikely to exhibit strong relationships between area occupied and overall abundance levels in all species. Where densities are more limited by physical habitat than by social behaviours, no strong tendency to range contraction and expansion with changing abundances should be expected. For example, poor relationships between stock area and abundance were reported for haddock on the Scotian Shelf (Marshall and Frank 1994) and for American plaice in the southern Gulf of St. Lawrence (Swain and Morin 1996). We suggest that the characterization of such tendencies may be key to understanding marine population dynamics, especially for those species under exploitation. In the simplest case, catchability increases with population declines in populations that

© 1997 NRC Canada

exhibit range occupation – abundance relationships, but remains constant in populations that do not (Paloheimo and Dickie 1964). Hence, differences in distribution properties can be expected to determine the most appropriate interpretation of fisheries data.

The survey data indicate that for northern cod, declines in occupied area preceded declines in biomass by approximately 2 yr with stock area declines beginning in 1989 without evidence of biomass declines until 1991. This finding supports earlier work (deYoung and Rose 1993; Rose et al. 1994; Warren 1997) reporting that the relatively stable population structures evident throughout the 1980s changed beginning in 1989.

Our analyses confirm that southward and seaward distribution changes of the northern cod stock have occurred since about 1988, and that lesser southward movements occurred in the cold years 1984 and 1985 (Rose et al. 1994). These results do not support the contentions of Hutchings and Myers (1995) that no movements have occurred. An hypothesis arising from our conclusions is that cod became concentrated in the southern reaches of their range in late 1989 and early 1990. Under this hypothesis, increased local densities would have led to increases in fishing mortality and catchability for both Canadian and non-Canadian vessels such that offshore trawler catch rates remained high, or even increased, during the period of abundance decline. It is noteworthy that an atypically large and dense aggregation of cod comprising a large portion of the full stock was located in the southern range in the area known as the "Bonavista corridor" in the spring of 1990 (Rose 1993; Rose et al. 1995). In this connection, the southward shifts in range that occurred in 1984 and 1985 were not accompanied by declines in occupied range. We believe that this finding is key to interpretations of the similarities and differences between the 1984–1985 and the post-1989 southward distribution shifts that both occurred during cold periods (Rose et al. 1994). The reasons for these differences are not known.

The statistical ellipse technique provides a straightforward method by which distribution data can be visualized and quantified. Bidirectional centroid positions may be assessed in relation to latitude and longitude simultaneously, and hence contain more information than unidirectional weighted averages of latitude (Rose et al. 1994). Moreover, the ellipse method appears to provide, for the limited data series available for northern cod, an index of stock status that has the potential to capture trends in stock size. In this connection, it is noteworthy that the ellipse area index was not anomalously high in 1986 as was the research survey abundance estimate (nor was the area containing 90% of the biomass). Thus, these techniques may be useful in assisting interpretation of research survey results, helping to overcome some of the difficulties associated with stock evaluations using only a single research survey abundance index.

A potential problem with the scale of our analysis could occur if the northern cod do not move in relative unison over their full range (the bivariate means would then not capture the full reality of distribution patterns and shifts). This problem was pointed out by Rose et al. (1994) in their earlier analysis, but the current state of knowledge of stock structures and differential migration patterns does not enable us to investigate distributional properties at scales smaller than the full distributional area (2J3KL). The 90% area method should not be affected by within-stock spatial heterogeneity. The need for a fuller understanding of the population structure of northern cod is evident.

Our data do not enable us to directly address causes of the observed range contraction. However, a few comments are in order. The contractions took place during a period of intense cooling on the northeast Newfoundland and Labrador shelves after 1989 (Colbourne and Narayanan 1994). Swain and Kramer (1995) suggested that cod in the Southern Gulf of St. Lawrence exhibited density-dependent shifts in spatial distribution patterns relative to thermal conditions. Shifts in cod distribution patterns relative to sea temperatures on the Grand Bank and northeast Newfoundland Shelf (NAFO divisions 3KL) have been postulated in early accounts of the fisheries (Close, undated) and more recently confirmed (O.V. Gerasimova, unpublished data). Perhaps cooling waters might account for the southerly concentration of cod during periods of intense cooling. It is noteworthy that the area where the cod concentrated in the years 1990–1992 on the northeast shelf had the highest bottom temperatures within the stock range in those years (G.A. Rose, unpublished data).

In conclusion, using traditional distribution methods and a statistical ellipse technique new to fisheries science, we have shown that cod distribution patterns and abundance levels have not been independent during the past 13 yr. Cod distributions have not only shifted north and south in association with overall thermal conditions (Rose et al. 1994), but have contracted with declining abundance levels. Moreover, distribution changes preceded abundance changes. We advance the hypothesis that northern cod not only shifted their distribution, but also concentrated at elevated local densities in the southern ranges of the stock from 1990 to 1992. We believe that these distributional changes led directly to an increased vulnerability to the offshore and inshore fisheries which were concentrated in the southern area, and contributed to the rapid decline in stock abundance. Additional studies will be required to address these hypotheses.

Acknowledgments

The authors gratefully acknowledge the efforts of all seagoing staff of the Department of Fisheries and Oceans for their continuing efforts in collecting the data. This work was supported in part by the Northern Cod Science Program. We thank J. Carscadden and D. Swain for helpful comments on an earlier draft.

References

Anonymous. 1989. Advice for 1989 on the management of cod in divisions 2J3KL. CAFSAC Advisory Doc. 89/1.

Anonymous. 1992*a*. Advice on the management of cod in divisions 2J3KL. CAFSAC Advisory Doc. 92/2.

Anonymous. 1992*b*. Scientific Council reports. Northwest Atlantic Fisheries Organization, Dartmouth, N.S. pp. 23–44.

Baird, J.W., Bishop, C.A., Brodie, W.B., and Murphy, E.F. 1992. An assessment of the cod stock in NAFO Divisions 2J3KL. NAFO SCR Doc. 92/18. Ser. No. N2063.

Bishop, C.A., Murphy, E.F., Davis, M.B., Baird, J.W., and Rose, G.A. 1993. An assessment of the cod stock in NAFO Divisions 2J3KL. NAFO SCR Doc. 93/86. Ser. No. N2271.

© 1997 NRC Canada

Bishop, C.A., Anderson, J., Dalley, E., Davis, M.B., Murphy, E.F., Rose, G.A., Stansbury, D.E., Taggart, C., and Winters, G. 1994. An assessment of the cod stock in NAFO Divisions 2J+3KL. NAFO SCR Doc. 94/40. Ser. No. N2410.

Black, G.A. 1993. ACON data visualization software: user manual — version 7.14. (Available from G.A. Black, Department of Fisheries and Oceans, 1707 Lower Water St., P.O. Box 550, Halifax, NS B3J 2S7, Canada).

Close, A. undated. The North Atlantic and Gulf of St. Lawrence fishing grounds. Albert Close, International Fishing Chart Publisher, 16 York Road, Illford, London.

Colbourne, E., and Narayanan, S. 1994. Environmental conditions in Atlantic Canada, summer 1994 with comparisons to the long term average. DFO Atl. Fish. Res. Doc. 94/65.

Colbourne, E., deYoung, B., and Rose, G.A. 1997. Environmental analysis of Atlantic cod (*Gadus morhua*) migration in relation to the seasonal variations on the Northeast Newfoundland Shelf. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Crecco, V., and Overholtz, W.J. 1990. Causes of density-dependent catchability of Georges Bank haddock *Melanogrammus aeglefinus*. Can. J. Fish. Aquat. Sci. **47**: 385–394.

deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. **50**: 2729–2741.

Doubleday, W.G., and Rivard, D. 1981. Bottom trawl surveys. Can. Spec. Publ. Fish. Aquat. Sci. **47**: 385–394.

Gordoa, A., and Hightower, J.E. 1991. Changes in catchability in a bottom-trawl fishery for Cape hake (*Merluccius capensis*). Can. J. Fish. Aquat. Sci. **48**: 1887–1895.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment. Chapman & Hall, New York.

Hutchings, J., and Myers, R.A. 1995. What can be learned from the collapse of a renewable resource? Atlantic cod (*Gadus morhua*) of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. **51**: 2126–2146.

Lear, W.H., and Parsons, L.S. 1993. History and management of the fishery for northern cod in NAFO divisions 2J, 3K and 3L. *In* Perspectives on Canadian marine fisheries management. *Edited by* L.S. Parsons and W.H. Lear. Can. Bull. Fish. Aquat. Sci. **226**: 55–90.

Marshall, C.T., and Frank, K.T. 1994. Geographic responses of groundfish to variation in abundance: methods of detection and their interpretation. Can. J. Fish. Aquat. Sci. **51**: 808–816.

Murawski, S.A., and Finn, J.T. 1988. Biological bases for mixed-species fisheries: species co-distribution in relation to environmental and biotic variables. Can. J. Fish. Aquat. Sci. **45**: 1720–1735.

Myers, R.A., and Cadigan, N. 1995. Was an increase in natural mortality responsible for the collapse of northern cod? Can. J. Fish. Aquat. Sci. **52**: 1274–1285.

Myers, R.A., and Stokes, K. 1989. Density-dependent habitat utilization of groundfish and the improvement of research surveys. ICES C.M. 1989/D:15.

Paloheimo, J.E., and Dickie, L.M. 1964. Abundance and fishing success. Rapp. P.-v. Réun. Cons. Perm. Int. Explor. Mer, **155**: 152–163.

Petrie, B., Loder, J.W., Akenhead, S.A., and Lazier, J. 1992. Temperature and salinity variability on the eastern Newfoundland Shelf: the residual field. Atmos.-Ocean, **300**: 120–139.

Rose, G.A. 1993. Cod spawning on a migration highway in the north-west Atlantic. Nature (Lond.), **366**: 458–461.

Rose, G.A., and Leggett, W.C. 1991. Effects of biomass-range interactions on catchability of migratory demersal fish by mobile fisheries: an example of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **48**: 843–848.

Rose, G.A., Atkinson, D.B., Baird, J., Bishop, C.A., and Kulka, D.W. 1994. Changes in distribution of Atlantic cod and thermal variations in Newfoundland waters, 1980–1992. ICES Mar. Sci. Symp. **198**: 542–552.

Rose, G.A., deYoung, B., and Colbourne, E. 1995. Cod (*Gadus morhua*) migration speeds and transport relative to currents on the northeast Newfoundland shelf. ICES J. Mar. Sci. **52**: 903–913.

Smith, S.J., and Somerton, G.A. 1981. STRAP: a user-oriented computer analysis system for groundfish research trawl survey data. Can. Tech. Rep. Fish. Aquat. Sci. No. 1030.

Swain, D.P., and Kramer, D.L. 1995. Annual variation in temperature selection by Atlantic cod *Gadus morhua* in the southern Gulf of St. Lawrence, Canada and its relation to population size. Mar. Ecol. Prog. Ser. **116**: 11–23.

Swain, D.P., and Morin, R. 1996. Relationships between geographic distribution and abundance of American plaice (*Hippoglossoides platessoides*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **53**: 106–119.

Swain, D.P., and Sinclair, A.F. 1994. Fish distribution and catchability: what is the appropriate measure of distribution? Can. J. Fish. Aquat. Sci. **51**: 1046–1054.

Swain, D.P., and Wade, E.J. 1993. Density-dependent geographic distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**: 725–733.

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

SYSTAT. 1992. Statistics, version 5.2 edition. Systat, Inc., Evanston, Ill.

Warren, W.G. 1997. Changes in the within-survey spatio-temporal structure of the northern cod (*Gadus morhua*) population, 1985–1992. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Warren, W.G., Bohm, M., and Link, D. 1992. A statistical methodology for exploring elevational differences in precipitation chemistry. Atmos. Environ. **26A**(1): 159–169.

Watson, D.F. 1982. ACORD — automatic contouring of raw data. Comp. Geosci. **8**: 97–101.

Watson, G.F., and Philip, G.M. 1985. A refinement of inverse distance weighted interpolation. Geo-Processing, **2**: 315–327.

Winters, G.H., and Wheeler, J.P. 1985. Interaction between stock area, stock abundance, and catchability coefficient. Can. J. Fish. Aquat. Sci. **42**: 989–998.

© 1997 NRC Canada

Changes in the within-survey spatio-temporal structure of the northern cod (*Gadus morhua*) population, 1985–1992

William G. Warren

Abstract: The question of what effects the movement of fish during a research survey might have on the estimate of abundance is explored by attempting to separate the autocorrelation in the data into spatial and temporal components. In the case of the 1985–1992 fall survey data of northern cod (*Gadus morhua*), there appears to have been a breakdown in the spatial structure of the stocks coincident with the decline in their abundance. Although conjectural, the trend is consistent with what one might expect to see as a consequence of a declining availability of prey species.

Résumé : Nous étudions les effets que peuvent avoir les déplacements des poissons sur l'estimation de l'abondance lors de travaux de recherche, en tentant de décomposer l'autocorrélation que présentent les données en éléments spatiaux et éléments temporels. Dans le cas des données obtenues pour la morue du Nord (*Gadus morhua*) lors des études réalisées à l'automne des années 1985–1992, il semble qu'il y ait eu rupture dans la répartition spatiale des stocks — rupture qui aurait coïncidé avec la diminution de leur abondance. Bien que de nature conjecturale, cette tendance est compatible avec les conséquences prévisibles d'une réduction de la disponibilité des espèces proies.
[Traduit par la Rédaction]

Introduction

Research-vessel surveys for assessing the northern cod (*Gadus morhua*) stock, over the past 15 yr or so, have employed stratified random sampling, with the strata defined by depth. In most years the survey of each of the three NAFO Divisions, 2J, 3K and 3L, commonly abbreviated 2J3KL, covers a period of 2.5–3.5 wk. The data are analyzed conventionally for a stratified random design (e.g., Cochran 1977); in other words, there is a tacit assumption that, although there would be some movement of the fish during the period of the survey, the data can be treated as if fixed in space and time.

In recent years, there has been recognition that, for many marine populations, the density at a location is more likely to be similar to the density at a neighbouring location than one which is further away, i.e., there is some degree of spatial correlation. There has been a feeling that stock assessment could be improved if, somehow, this spatial correlation could be incorporated in the analysis. Unfortunately, there has also been the erroneous belief that the existence of spatial correlation causes the conventional design-based (stratified random) estimators to be biased (cf. Brus and de Gruijter 1993). This has given rise to an interest in the methods of spatial analysis, especially kriging, for the assesment of marine populations (e.g., Conan 1985; Conan et al. 1988*a*, 1988*b*; Conan and Wade 1989; Petitgas and Poulard 1989; Guillard et al. 1990; Anonymous 1991; Freire et al. 1991; Sullivan 1991; Simard et al. 1992, 1993; González-Gurriarán et al. 1993; Petitgas 1993). For the most part, these deal with relatively sedentary species, such as crab, or with acoustic surveys where the population under study is covered in a relatively short time period. Again, there is the tacit assumption that the spatial distribution as observed is fixed in time, at least for the period of the survey. This may be a reasonable assumption for the more sedentary species or some acoustic surveys.

The viability of applying spatial analysis to survey data of something as mobile as northern cod where, perforce, the survey extends over 2.5 wk or more is clearly open to question. Nevertheless, while there would appear to be little value in attempting to map the stock, it must be remembered that mapping is not necessarily a component of a spatial analysis; one can compute a kriged mean (or abundance estimate) without the construction of a map. The point is that the krigged mean, as well as spatial interpolation, depends on a measure of the spatial correlation, namely the variogram. It seems reasonable to assume that fish movement will affect the spatial structure and hence the variogram. In what follows, an approach is developed for separating and estimating the spatial and temporal components of trawl survey data, and is applied to the data from the research-trawl surveys of northern cod in NAFO Divisions 2J3KL for the years 1985–1992. The focus of this paper is on the changes in spatial structure revealed by this approach, these changes being coincident with the collapse of the northern cod stock.

Data

Stratified random research-trawl surveys of northern cod have been conducted in NAFO Divisions 2J3KL since 1977, 1978, and 1981, respectively. As noted above, the strata were defined by depth, and, until recently, sample allocation was proportional to stratum area, with the proviso that there should be at least two stations trawled in each stratum. In 1989, a two-phase design (Francis 1984) was instituted; in particular,

Received December 1, 1994. Accepted June 21, 1995.
J13227

W.G. Warren. Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

© 1997 NRC Canada

stations were added in those strata in which the larger catches occurred. Because of the potential for this strategy to yield biased estimates of abundance, in 1991 this adaptive procedure was replaced by conventional stratified random sampling, with stratum size based on the stratum catches of the previous 5 yr, again with the proviso that at least two stations were trawled in each stratum. In this paper, data from 1985 to 1992 are utilized. Although the stations added in 1989 and 1990 were subsequently excluded from the calculation of the official abundance estimates for those years, they do provide valid data for the purpose of the present study. However, trawls taken for other than survey purposes (e.g., searching, experimental, tagging) have been excluded, as well as trawls recorded as unsuccessful because of gear failure or other indications that the gear had not performed properly. Data are the catches in kilograms for a standard 30-min tow.

As noted above, the time taken to survey a division was generally of the order of 2.5–3.5 wk. For Divisions 2J and 3K, this was accomplished by three cruises; the first covered Division 2J, the second completed 2J and began 3K, and the third finished 3K. The proportion of 3K covered in the second cruise varied from year to year. From 1986 to 1990, Division 3L was covered by a single cruise and by two cruises in 1991 and 1992. In 1985, three cruises were employed covering a period of approximately 6 wk. In 3L, this year was also unique in the relatively large amount of area overlapped by the cruises. All other cases more or less followed the general pattern where, to minimize travel, the survey proceeded along one half of the division and then returned along the other half; accordingly, there was then little or no areal overlap, although there were several instances where a few stations sampled early in the survey were located relatively close to stations sampled near the end of the survey.

Spatio-temporal model

Let $Z(s_i)$ denote the catch (biomass) at location s_i. The *intrinsic hypothesis* commonly assumed for kriging is that $E[Z(s+h) - Z(s)] = 0$ and $\mathrm{Var}[Z(s+h) - Z(s)] = 2\gamma(h)$ where h is the distance between the points s and $s+h$. Recall that these expectations are taken with respect to an assumed underlying stochastic process. The function $\gamma(h)$ is the variogram, referred to above, and depends solely on the distance h. Accordingly, one generally goes about estimating the variogram by calculating $[Z(s_i)-Z(s_j)]^2/2$ for all possible station pairs s_i, s_j in the sample. In practice, these are commonly grouped and averaged by distance classes (e.g., Cressie 1991, p. 75, who also gave robust alternative estimators of the variogram).

In a research survey, each trawl is made at a different time and place. Thus, let $Z(s_{ij})$ denote the catch made at location s_i at time j. For convenience, let us abbreviate $Z(s_{ij})$ to Z_{ij}. Then, any pair of observations can be written Z_{ij} and $Z_{i'j'}$ where $i \neq i'$ and $j \neq j'$.

If we regard $Z_{1j}, Z_{2j}, \ldots$ and $Z_{1j'}, Z_{2j'}$ as two realizations of the same stochastic process, we have $E[Z_{ij} - Z_{i'j}] = 0$, all j, and $\mathrm{Var}[Z_{ij} - Z_{i'j}] = 2\gamma(h_{ii'})$, all j, where $h_{ii'}$ is the distance between s_i and $s_{i'}$. It may also be reasonable to assume that, over time, the catches at any one location would form a stationary time series, or specifically that $E[Z_{ij} - Z_{ij'}] = 0$, all i, and $\mathrm{Var}[Z_{ij} - Z_{ij'}] = 2\gamma_t(t_{jj'})$ where $t_{jj'}$ denotes the time between the catches and $\gamma_t(t)$ is a function of t only, i.e., a "temporal" variogram. It will be convenient to write the "spatial" variogram as $\gamma_h(h)$.

Consider, then, $Z_{ij} - Z_{i'j'} = Z_{ij} - Z_{i'j} + Z_{i'j} - Z_{i'j'}$. It follows that

$$E[Z_{ij} - Z_{i'j'}] = 0$$

and

$$\mathrm{Var}[Z_{ij} - Z_{i'j'}] = 2\gamma_h(h_{ii'}) + 2\gamma_t(t_{jj'}) + 2\mathrm{Cov}[(Z_{ij} - Z_{i'j}), (Z_{i'j} - Z_{i'j'})].$$

If the temporal component of the stochastic process is independent of the spatial component, then the difference between the catches at different stations at the same time will be independent of the difference between catches at the same station but at different times; thus, for the time being, we shall assume $\mathrm{Cov}[(Z_{ij} - Z_{i'j}), (Z_{i'j} - Z_{i'j'})] = 0$, and

$$\mathrm{Var}[Z_{ij} - Z_{i'j'}] = 2\gamma_h(h_{ii'}) + 2\gamma_t(t_{jj'})$$

or

$$\gamma(|s_{ij} - s_{i'j'}|) = \gamma_h(h_{ii'}) + \gamma_t(t_{jj'})$$

where $|s_{ij} - s_{i'j'}|$ denotes the "distance" between s_{ij} and $s_{i'j'}$. The problem is that we do not know how to weight geographical distance with time. Idealistically, one might have $|s_{ij} - s_{i'j'}| = \sqrt{h_{ii'}^2 + k^2 t_{jj'}^2}$ but k remains unknown.

The spatial component, $\gamma_h(h)$, could be estimated if catches were made simultaneously at a sufficiently large number of stations; this, however, is logistically impossible. We could also estimate $\gamma_t(t)$ from a sufficiently large number of catches made at the same locations. While this may be more feasible in theory, sampling in a stratified random survey is done without replacement, so that no location is sampled more than once. Nevertheless, it may be possible to approximate $\gamma_h(h)$ and $\gamma_t(t)$ by grouping the $(Z_{ij} - Z_{i'j'})^2/2$ jointly by sufficiently narrow distance and time intervals. However, the nature of the data, to some extent, works against this. For reliable estimation of the variogram, a certain number of data locations are required (and it is preferable that these be uniformally spaced). Experience suggests that this number is about 150 (R. Webster, ETH Zurich, Switzerland, personal communication). This is roughly the number of stations sampled in each division. However, the dispersal of the stations is far from regular, and while this number may be adequate for a spatial variogram, it is questionable whether this remains so when the data have to be partitioned spatially and temporally. Also, there is a limit to the distance between stations sampled within a reasonably short time interval. Further, because of travel time considerations, most stations that are geographically close are sampled within a relatively short time period. The data are, thus, far from ideal for our purpose but they are, perforce, what we have to work with.

The distribution of trawl biomass tends to be strongly positively skewed. Let y denote the trawl biomass and assume that it is, in fact, lognormally distributed. Then, $x = \log(y)$ and, in an obvious notation, $\mu_y = \exp(\mu_x + \sigma_x^2/2)$ and $\sigma_y^2 = \mu_y^2[\exp(\sigma_x^2) - 1]$. The variograms will, in general, be

© 1997 NRC Canada

constructed from the logarithmically transformed data. Thus, differences in the transformed scale correspond to ratios of the untransformed catches.

The introduction of logarithmic transformation highlights the problem of zero catches, the actual proportion in the surveys of 2J3KL between 1985 and 1992 ranging from about 5 to 50%.

The delta-distribution (Aitchison and Brown 1957) has been suggested by Pennington (1983) as a potentially suitable model for describing the distribution of catch-per-tow data from trawl surveys for fish and plankton. The motivation for this stems from the fact that any particular species occupies only part of the total survey area, whence zero catches come about from trawling in areas of unsuitable or otherwise unoccupied habitat. In formal terms:

$$P(Y < 0) = 0$$

$$P(Y = 0) = \delta$$

$$P(y < Y < y + dy) = \lambda(y)dy,\ 0 < y$$

where $\lambda(y)$ denotes the lognormal density function.

We therefore consider a two-phase process; first, we introduce an indicator variable that takes the value 1 if the location is occupied and the value 0 if unoccupied. Second, we analyze the catches conditional on the location being occupied.

We define an indicator variable by $I(s) = 1$ if $Z(s_{ij}) > 0$ and $= 0$ if $Z(s_{ij}) = 0$, and, again for convenience, let us write I_{ij} for $I(s_{ij})$. In a manner parallel to the development presented above, with the I_{ij} playing the role of the Z_{ij}, we assume that there exist spatial and temporal components of the indicator variogram, $\gamma_I(|s_{ij} - s_{i'j'}|) = (1/2)\mathrm{Var}[I_{ij} - I_{i'j'}]$, and the components can be estimated by considering sufficiently narrow slices of distance and time.

Under stationarity, $E[I_{ij} - I_{i'j'}] = 0$. Thus, $\mathrm{Var}[I_{ij} - I_{i'j'}] = E[(I_{ij} - I_{i'j'})^2]$. Now, $|I_{ij} - I_{i'j'}|$ can take only one of two values, 0 and 1: 0 when both I_{ij} and $I_{i'j'} = 1$ or both $= 0$, and 1 when either I_{ij} or $I_{i'j'} = 0$ and the other $= 1$. In the first case, both locations fall in either an occupied or an unoccupied area; in the second case, one location falls within an occupied area and the other within an unoccupied area. Thus, $2\gamma(|s_{ij} - s_{i'j'}|)$ can be interpreted as the probability that one location falls within an occupied area and the other within an unoccupied area. It follows that if the locations are close in both time and distance, it would be expected that both would be inside or outside an aggregation of fish, and thus the probability that $|I_{ij} - I_{i'j'}| = 1$ be small. In what follows, it will be convenient to think of the spatial and temporal components in terms of this probability.

Now each $(I_{ij} - I_{i'j'})^2 = |I_{ij} - I_{i'j'}|$ can be allocated to the (r, c) cell of an array P representing the discretized distance–time space, where the binning procedure is defined by $r = [h_{ii'}/w_h] + 1$, $c = [t_{jj'}/w_t] + 1$, where $[y]$ denotes the greatest integer less than or equal to y (here necessarily nonnegative) and w_h, w_t are the widths of the distance and time classes, respectively. Let n_{rc} denote the number of $|I_{ij} - I_{i'j'}|$ that fall in the (r, c) cell and suppose that x_{rc} of these are 1. Let p_{rc} be the probability that one of the locations belonging to the (r, c) cell will fall in an occupied area and the other in an unoccupied area. The likelihood will then be

$$\prod \binom{n_{rc}}{x_{rc}} p_{rc}^{x_{rc}} (1 - p_{rc})^{n_{rc} - x_{rc}}.$$

The maximum likelihood extimates of the p_{rc} are, of course, x_{rc}/n_{rc}.

By analogy with contingency tables, for separate spatial and temporal components we would require $p_{rc} = p_{r.}p_{.c}$. The log likelihood equations then become

$$\sum_c \frac{x_{rc}}{p_{r.}} - \sum_c \frac{(n_{rc} - x_{rc})p_{.c}}{1 - p_{r.}p_{.c}} = 0$$

$$\sum_r \frac{x_{rc}}{p_{.c}} - \sum_r \frac{(n_{rc} - x_{rc})p_{r.}}{1 - p_{r.}p_{.c}} = 0.$$

These equations are readily solved by the Newton–Raphson method; convergence is quite rapid. Very occasionally, $\sum_c x_{rc} = 0$ or $\sum_r x_{rc} = 0$ in which case $p_{r.}$ or $p_{.c}$, respectively, are taken as zero.

In the second phase, to estimate the spatial and temporal variogram components conditionally on $Z_{ij} > 0$, analogously to the indicator variogram above, the $[\log(Z_{ij}) - \log(Z_{i'j'})]^2$ are averaged by distance–time cells.

The average of the $[\log(Z_{ij}) - \log(Z_{i'j'})]^2/2$ in a cell approximates $\gamma(|s_{ij} - s_{i'j'}|)$ and is allocated to the (r, c) cell of an array D where, as above, $r = [h_{ii'}/w_h] + 1$, $c = [t_{jj'}/w_t] + 1$. Since it is assumed that $\gamma(|s_{ij} - s_{i'j'}|) = \gamma_h(h_{ii'}) + \gamma_t(t_{jj'})$, it follows that the (r, c) element of D can be written $\alpha_r + \beta_c$. Unbalanced two-way analysis of variance may therefore be used to estimate the α_r and β_c. (Note that the procedure is used here simply to esimate the α_r and β_c and not for any tests of hypotheses. If there were n values of $Z_{ij} > 0$, there would be $n(n + 1)/2$ "observations" going into the analysis; these are certainly not independent.) Since, as it stands, the model is overparameterized, only the differences $\alpha_r - \alpha_{r'}$ and $\beta_c - \beta_{c'}$ can be estimated. However, if the (r, c) element of D is taken as $\mu + \alpha_r + \beta_c$ and the constraints $\sum_r \alpha_r = 0$, $\sum_c \beta_c = 0$ imposed (which does not affect the estimates of the differences) the μ, α_r, and β_c can be estimated; $\hat{\mu} + \hat{\alpha}_r$ will be taken as estimating the spatial component of the variogram at the distance corresponding to r, and $\hat{\beta}_c$ as measuring by how much the spatial variogram is perturbed at the time corresponding to c.

The above, of course, gives the appearance of a *non sequitur*. The $\mu + \alpha_r$ appear to be playing the role of the $\gamma_h(.)$ and the β_c of the $\gamma_t(.)$. But $\gamma_t(t_{jj'}) = \mathrm{Var}[Z_{ij} - Z_{ij'}]/2$ which is > 0 whereas the constraint $\sum \beta_c = 0$ implies at least one β_c is less than zero (unless all equal 0). This has no effect on the $\mu + \alpha_r + \beta_c$; it means that part of the μ should be apportioned to the spatial component and part to the temporal component.

Results

Indicator variable

We begin by considering the estimates of the spatial component of the indicator variable, $\hat{p}_{r.}$ (Fig. 1). (The years 1986 and 1989 in Division 3K have been omitted because of very few zero catches.) The widths of the distance and time classes, w_h and w_t, were taken as 6 nautical miles (nm)

© 1997 NRC Canada

Fig. 1. Typical examples of the spatial component, $\gamma_h(h)$, of the variograms for the indicator variable. The spherical form is fitted by weighted least squares. The distance classes, h, are in nautical miles (nm). (*a*) Division 2J, 1985; (*b*) Division 3L, 1986; (*c*) Division 3K, 1990; (*d*) Division 2J, 1992.

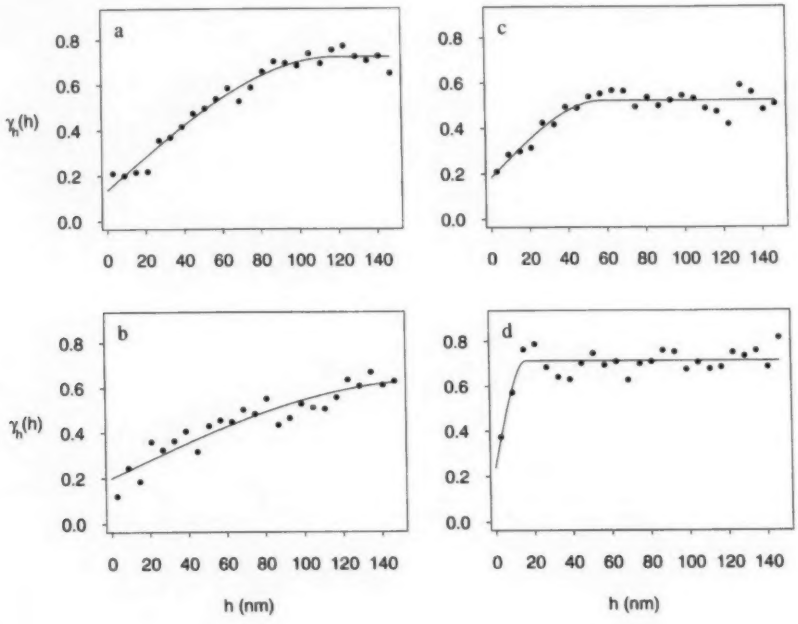
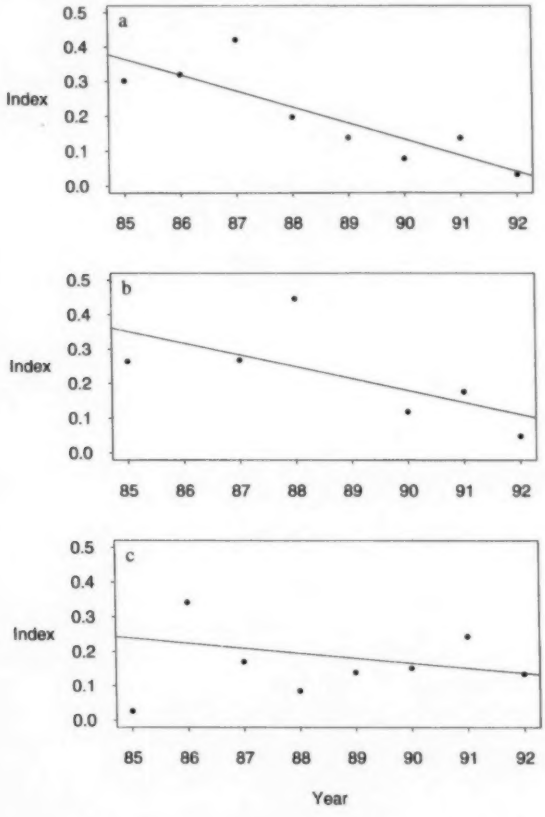


Table 1. Parameters (nugget, sill, and range, nautical miles (nm)) of the spherical variogram fitted to the spatial component of the indicator variable (No. refers to the number of distance classes used in the fit; Index refers to a measure of departure from a purely random variogram).

Division	Year	No.	Nugget	Sill	Range (nm)	Index
2J	1985	25	0.135	0.723	118.6	0.302
	1986	25	0.224	0.711	151.0	0.320
	1987	25	0.158	0.738	179.6	0.421
	1988	25	0.277	0.617	114.6	0.197
	1989	20	0.241	0.667	69.1	0.138
	1990	20	0.232	0.627	40.0	0.079
	1991	25	0.356	0.757	113.5	0.138
	1992	25	0.237	0.713	16.1	0.034
3K	1985	25	0.146	0.626	110.0	0.264
	1987	25	0.057	0.414	25.4	0.268
	1988	25	0.055	0.434	168.5	0.446
	1990	25	0.183	0.522	58.3	0.118
	1991	25	0.154	0.603	75.8	0.176
	1992	20	0.486	0.678	54.1	0.048
3L	1985	20	0.440	0.534	149.2	0.027
	1986	25	0.199	0.631	164.0	0.342
	1987	20	0.096	0.378	73.4	0.171
	1988	25	0.105	0.461	35.3	0.085
	1989	25	0.164	0.606	61.1	0.139
	1990	20	0.158	0.436	76.5	0.152
	1991	20	0.313	0.691	143.8	0.244
	1992	25	0.306	0.682	77.6	0.134

© 1997 NRC Canada

Fig. 2. Plots of the index measuring the departure from pure noise of the spatial component of the variogram of the indicator variable against year. Trend lines are fitted by ordinary least squares with 1985 omitted in Fig. 2*c*. (*a*) Division 2J; (*b*) Division 3K; (*c*) Division 3L.



(equivalent to 0.1° of latitude) and 12 h, respectively. These seemed a reasonable compromise between making the intervals as narrow as possible while still maintaining an adequate number of paired locations per cell. The distances were restricted to a maximum of 150 nm and 360 h; this resulted in a 25 × 30 array, although some cells were empty.

In most cases the estimated spatial variogram is well fitted by a spherical variogram (Fig. 1):

$$\gamma_h(h) = 0, \quad h = 0$$
$$= c_0 + c_1(3h/a - (h/a)^3)/2, \quad 0 < h \le a$$
$$= c_0 + c_1, \quad h > a$$

where c_0 denotes the nugget, $c_0 + c_1$ the sill, and a the range. In some cases the last few points were erratic or failed to follow the trend, and in a couple of cases the procedure used (non-linear least squares) failed to converge. In all cases, however, a spherical variogram could be fitted to the first 20 points. The estimates (Table 1) are based either on the first 20 points, or all 25 points, in those cases where the exclusion of the last five points would make neglible difference.

Table 2. Values of the statistic W for testing for trend in the temporal component of the variogam for the indicator variable (the two-sided 1, 2, 5, and 10% critical values are 0.85, 0.88, 0.92, and 0.96, respectively).

	Division		
Year	2J	3K	3L
1985	0.598	0.768	0.805
1986	0.882	—	0.539
1987	0.607	0.708	0.362
1988	0.603	0.412	0.426
1989	0.849	—	0.683
1990	0.506	0.560	0.577
1991	0.885	0.535	0.401
1992	1.012	0.704	0.812

What we seem to be seeing is a gradual transition over time from a well-defined variogram, with relatively large range and small nugget, to something approaching a purely random variogram. To quantify this, we calculate $1 - \int_0^H \gamma_h(h)dh/(c_0 + c_1)$ as a measure of the departure from a purely random variogram. These values are also given in Table 1 with H taken as 120 nm.

The trend is most clearly observed in Division 2J and to a somewhat lesser extent in Division 3K; it is questionable whether there is a trend in Division 3L (Fig. 2). It is noted that the collapse of the stock is reputed to have begun in the north (Division 2J) and progressed south. (The results for 3L 1985 seem the most out of line; recall that this survey was conducted somewhat differently from the others in that three cruises took place over approximately a 6-wk period with some overlap of the areas covered by each. It is tempting to conjecture that this is the cause of the atypical result for that division and year and, accordingly, 3L 1985 has been omitted from the regression in Fig. 2.)

In contrast, one does not see, in general, any monotonic trend in the estimates of the temporal component, $\hat{p}_{.c}$, but rather a tendency for oscillation (Fig. 3). To test whether the points form something other than a random sequence, for each division and year the statistic

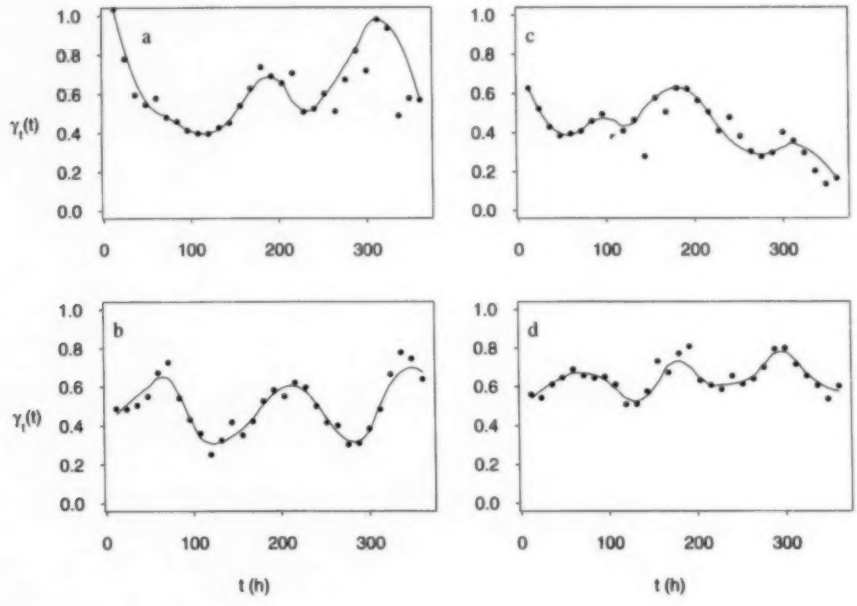
$$W = \left[\sum |\hat{p}_{.c+1} - \hat{p}_{.c}|/(n_t - 1)\right]/s$$

was calculated where $s^2 = \sum(\hat{p}_{.c} - \bar{\hat{p}})^2/n$ and $\bar{\hat{p}}$ is the average of the $\hat{p}_{.c}$ (Table 2). The null distribution of this statistic under the assumption that the observations are indepedently normally distributed has been examined by Kamat (1953) who gave one-sided upper and lower 0.5, 1, 2.5, and 5% critical values (reproduced in Table 2).

It will be seen that, with one exception, all values are significant at the 5% level, and indeed 19 of the 22 values are significant at the 1% level or better. Notably, the one case of nonsignificance is 2J 1992; the second highest value for 2J occurs in 1991 and the highest value for 3L also in 1992. Note that the inferences depend on the assumption that the observations are from a normally distributed variable. Even if this were not strictly the case, rejection of the null hypothesis seems well established, for almost all years and divisions. In

© 1997 NRC Canada

Fig. 3. Typical examples of the temporal component, $\gamma_t(t)$ of the variograms for the indicator variable with the fits given by robust locally weighted regression. The time classes, t, are measured in hours. (*a*) Division 2J, 1985; (*b*) Division 3K, 1990; (*c*) Division 3L, 1990; (*d*) Division 3K, 1992.



other words, the points do not represent random sequences but embody some form of trend.

To obtain a better idea of the nature of the trend, the data were smoothed by use of a robust locally weighted regression (Cleveland 1979) with, in Cleveland's notation, $d = 2$, $f = 0.2$, $W(x) = (1 - |x|^3)^3$, $|x| < 1$ and $= 0$ otherwise, $B(x) = (1 - x^2)^2$, $|x| < 1$ and $= 0$ otherwise. The smoothed values show little in the way of common characteristics other than, in most cases, some degree of irregular oscillation (Fig. 3). There does, however, seem to be a trend in recent years towards higher average values with a smaller variation. In confirmation of this the average of the smoothed values is plotted against year, along with the least squares regression (Fig. 4), and likewise for the amplitude, i.e., the difference between the maximum and minimum of the smoothed values (Fig. 5). (Again, 1985 3L is omitted from the calculations.)

The oscillatory behaviour of the $p_{.c}$ can be rationalized as follows. Consider two fixed locations. At time zero, let one be in an unoccupied area and the other within an occupied area; this can be thought of as being outside and inside a school of fish. This is a 0,1 situation. If the school is sufficiently large, as the school moves the point initially outside the school will be enveloped by the school, while that initially within the school remains within it. This is a 1,1 situation. As time progresses, the school will have passed over this second point, which is now outside the school, but the other point remains within the school. This is a 1,0 situation. Next, if the distance between schools is sufficiently large, both locations will lie outside the school, i.e., the 0,0 situation. As the next school approaches, it will first envelope one of the points and the cycle is repeated. This is, of course, somewhat idealistic, but since fish do tend to move in schools, what is being observed in the temporal variogram would appear to be the integration of components of this type. Clearly, the survey could start at any part of any of the cycles.

Nonzero catches

Let us now turn to the results based on the use of the $\log(Z_{ij})$ for $Z_{ij} > 0$. The widths of the distance and time classes were the same as for the indicator variable. As noted above, while the analyses of variance, as they stand, cannot be used for hypothesis testing, they do provide a measure of the relative importance of the spatial and temporal effects and their "interaction". Compared with the "within-cell" mean squares the F-ratios for interaction range from 0.88 to 1.94. The frequencies of the F-ratios for the spatial and temporal effects are given in Table 3. This suggests that the temporal components are at least as "significant" as the spatial and that both, for the most part, dominate the interaction, which corresponds to $\mathrm{Cov}((Z_{ij} - Z_{i'j}),(Z_{ij'} - Z_{i'j'}))$, and, for practical purposes, can here be regarded as random "noise".

In most cases the estimated variogram, $\hat{\mu}+\hat{\alpha}_r$, is well fitted by the spherical form (Fig. 6). Fitting was accomplished by weighted least squares; in three cases the fit degenerated to a linear variogram. (The weights were taken as proportional to the inverse of the estimated variance of the $\hat{\mu} + \hat{\alpha}$ (e.g., Chakrabarti 1962).) The first 20 distance classes were used, although because of the relatively low weights given to the final five points, with only one expection, fits to all 25 distance classes differ negligibly from these. A measure of departure from a purely random variogram was calculated in the same manner as for the indicator variable (Table 4). (In the

© 1997 NRC Canada

Fig. 4. Plots of the mean of the fitted temporal component of the variogram for the indicator variable against year. Trend lines are fitted by ordinary least squares with 1985 omitted from Fig. 4*c*. (*a*) Division 2J; (*b*) Division 3K; (*c*) Division 3L.

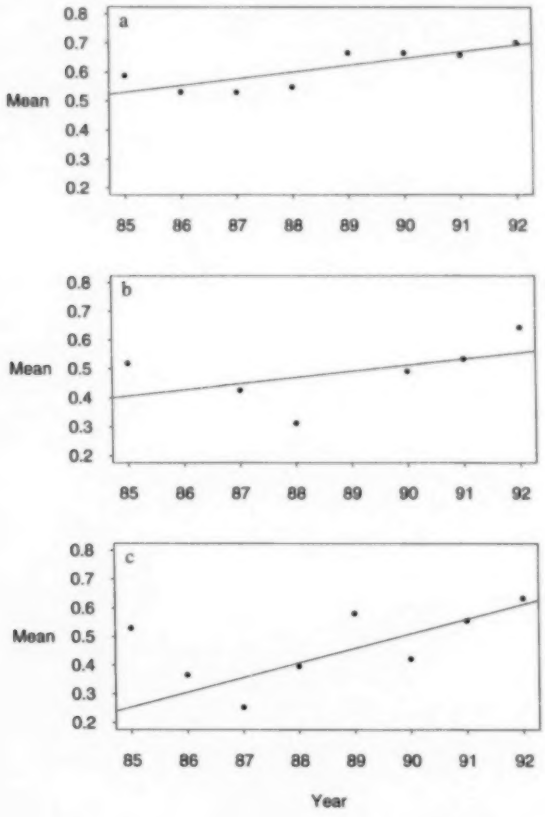


Fig. 5. Plots of the amplitude (maximum – mininum) of the fitted temporal component of the variogram for the indicator variable against year. Trend lines are fitted by ordinary least squares with 1985 omitted from Fig. 5*c*. (*a*) Division 2J; (*b*) Division 3K; (*c*) Division 3L.

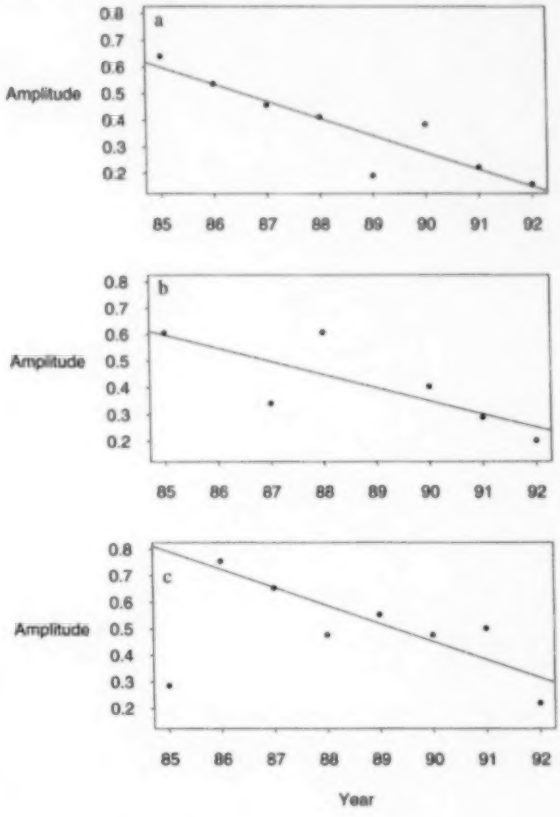


Table 3. Frequency of F-ratios from analyses of variance used for estimating the spatial and temporal components of variograms of nonzero catch data. (note: these are presented to illustrate the relative magnitude of the spatial and temporal effects; conventional p-values are innappropriate).

Range of F	Spatial	Temporal
1–2	5	3
2–3	6	4
3–4	1	1
4–5	4	3
5–6	5	3
6–7	1	—
7–8	1	3
8–9	—	2
9–10	1	2
> 10	—	3

case of a linear variogram, c_0+c_1h, the index was calculated, analogously, as $1-c_1/(c_0+2c_1)$.)

As with the indicator variable, an approach towards a purely random variogram in the more recent years can be observed for, in particular, 2J and 3L (Fig. 7). This is of more than passing interest in that the indicator variogram was based on absence–presence (0,1) data whereas the variograms (Table 4) are based on the (logarithm of) catch biomass conditional on the biomass being > 0.

Estimates of the temporal components, the $\hat{\beta}_c$, again do not appear to represent random sequences (Fig. 8). This is confirmed by the statistic W (Table 5) of which only one would be judged as not significant (5% level) and 17 of the 24 as significant at the 1% level.

The smoothed estimates obtained by robust locally weighted regression, with d, f, $W(x)$, and $B(x)$ as above (Fig. 8), show the same kind of irregular oscillation as the temporal component of the indicator variable. Although we are now dealing with $\log(Z_{ij})$ conditional on Z_{ij} being > 0, the oscillation can be rationalized in a manner parallel to that given above, if the density of fish in an aggregation is at its lowest near the

© 1997 NRC Canada

Fig. 6. Typical examples of the spatial component, $\gamma_h(h)$ of the variograms for the nonzero catches. The spherical form is fitted by weighted least squares. The distance classes, h, are in nautical miles (nm). (*a*) Division 3L, 1985; (*b*) Division 3L, 1990; (*c*) Division 3K, 1986; (*d*) Division 2J, 1986.

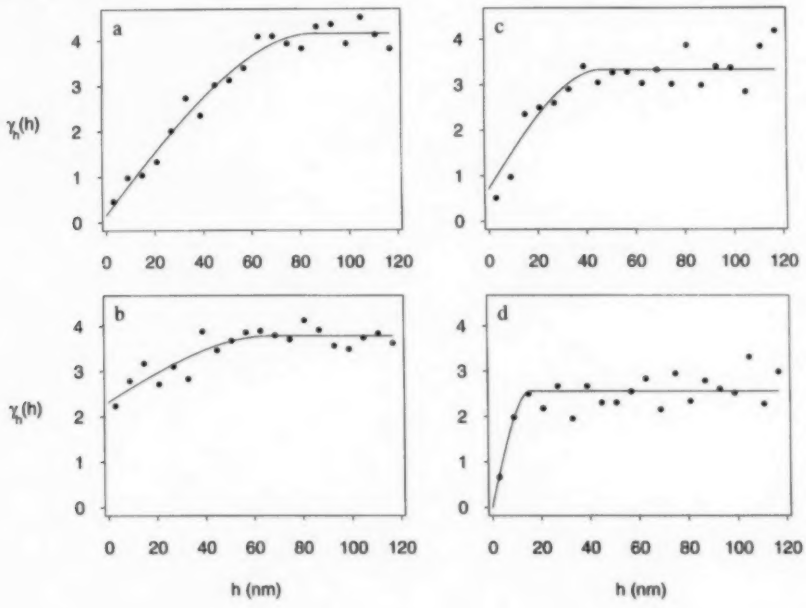


Table 4. Parameters (nugget, sill, and range, nautical miles (nm)) of the spherical variogram fitted to the spatial component of the nonzero catches (Index as in Table 1).

Division	Year	Nugget	Sill	Range (nm)	Index
2J	1985	1.504	3.183	91.9	0.152
	1986	0	2.558	15.6	0.049
	1987	1.552	0.683	—[a]	0.234
	1988	1.732	4.792	111.6	0.223
	1989	1.971	5.722	69.6	0.142
	1990	3.487	5.539	59.8	0.069
	1991	1.964	2.836	27.7	0.027
	1992	0.934	1.351	26.2	0.026
3K	1985	0.904	2.343	54.8	0.105
	1986	0.712	3.333	46.3	0.114
	1987	1.537	0.841	—[a]	0.258
	1988	1.678	3.913	182.8	0.310
	1989	2.031	3.431	53.5	0.068
	1990	3.656	6.400	93.4	0.122
	1991	0.821	4.421	50.7	0.129
	1992	0.118	1.152	30.5	0.086
3L	1985	0.156	4.144	86.4	0.260
	1986	1.498	3.440	74.8	0.132
	1987	0.066	3.365	102.0	0.312
	1988	0.967	3.559	164.1	0.364
	1989	0.491	3.664	104.2	0.282
	1990	2.321	3.782	67.0	0.081
	1991	2.502	0.628	—[a]	0.167
	1992	2.094	3.773	14.3	0.020

[a]Denotes linear variogram, intercept, and slope.

boundary of the aggregation and increases towards its centre. Such school structure seems likely.

It is difficult to discern any trend in the smoothed temporal components similar to that observed for the temporal components of the indicator variable. However, the smallest amplitude occurs with 2J 1992 and the third smallest with 3K 1992. We return to this point in the Discussion.

Discussion

The above analyses suggest a trend from a population with strong spatial structure (positive spatial correlation extending 60+ nm) in the middle 1980's to a population with little or no spatial structure in 1992. The estimated temporal components for the indicator variable give the impression of a change from relatively slow movement of large aggregations in the the 1980's to rapid movement of smaller aggregations in 1992. These two components, although constructed as independent, are interrelated conceptually; one may well expect to see a stable spatial structure in slices taken at different times from a population formed of large, slow-moving aggregations. Conversely, it would seemingly be difficult to see any spatial pattern in a population made up of small, fast-moving, aggregations. That a change in the temporal pattern is better discerned with the indicator variable than the nonzero catches may simply reflect a more diffuse movement within aggregations than the movement of aggregations as a whole.

Apart from the results for 3L 1985 (which, as noted above, may stem from the different manner in which that survey was conducted) the most anomalous results are, perhaps, those of the nonzero catches in 1986, for, in particular, 2J and 3L

© 1997 NRC Canada

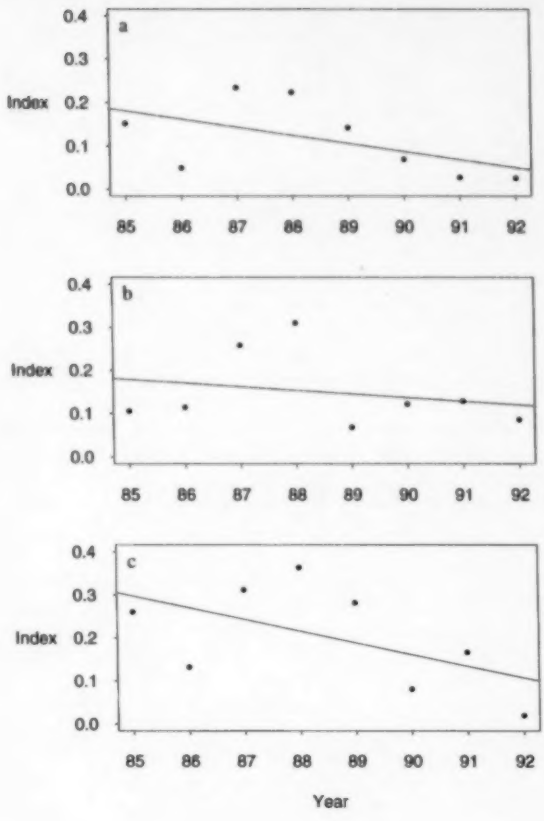


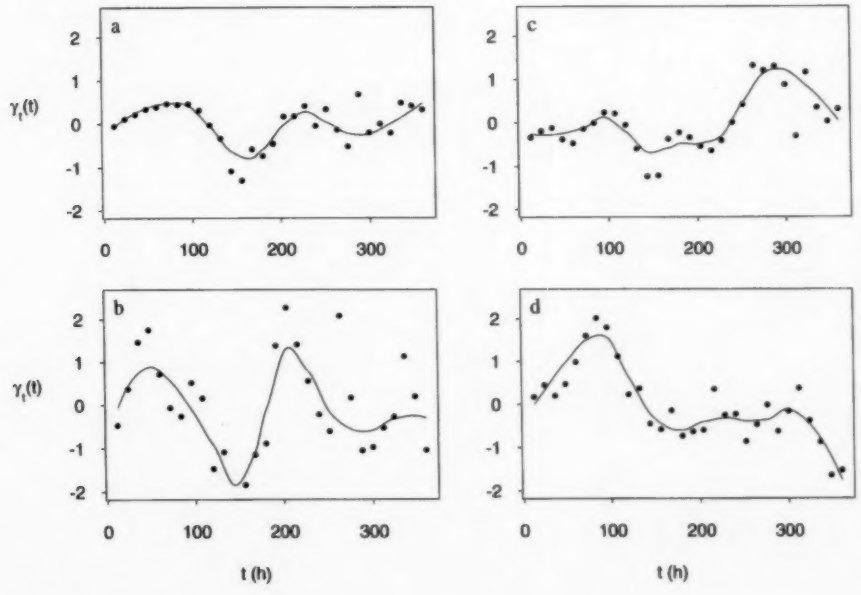
Fig. 7. Plots of the index measuring the departure from pure noise of the spatial component of the variogram for nonzero catches against year. Trend lines are fitted by ordinary least squares. (*a*) Division 2J; (*b*) Division 3K; (*c*) Division 3L.

(Fig. 7) where, especially for 2J, the variograms appear to be closer to random noise than expected from the general trend over years. This suggests relatively more within-aggregation movement, while for that year the movement of the aggregations as a whole seems as expected (Fig. 2). The 1986 estimate of abundance was unusually high; this could be a consequence of the very high sampling error indicated by simulation (Warren 1994), but one is tempted to conjecture that the movement may have resulted in a greater proportion of the fish getting in the path of the trawl than usual.

The trends are coincident with the collapse of the northern cod stock. They indicate that, as well as a simple reduction in numbers and/or biomass, the decline also involves a change in the spatio-temporal structure of the population.

One cannot determine the reason(s) for these changes in the spatio-temporal stucture, over the years in question, from the trawl data per se; one can only conjecture what these might be. Consider the following scenario. Suppose initially that prey species are plentiful in the usual feeding grounds. One would then expect the cod population to exhibit a stable spatial distribution. It would be strongly aggregated around the more favourable feeding centres and gradually decrease with distance from these centres. This may be coupled with a migratory drift. Suppose that over time the prey becomes scarce. There would still be some aggregation about feeding centres that are reduced in size and possibly number, but

Fig. 8. Typical examples of the temporal component, $\gamma_t(t)$, of the variograms for the nonzero catches with the fits given by robust locally weighted regression. The time classes, t, are measured in hours. (*a*) Division 3K, 1987; (*b*) Division 3K, 1986; (*c*) Division 2J, 1987; (*d*) Division 3L, 1988.



© 1997 NRC Canada

Table 5. Values of the statistic W for testing for trend in the temporal component of the variogam for the nonzero catches (critical values are as in Table 2).

Year	2J	3K	3L
1985	0.601	0.865	0.953
1986	0.955	0.787	0.694
1987	0.575	0.674	0.633
1988	0.919	0.632	0.526
1989	0.614	0.662	0.912
1990	0.802	1.087	0.444
1991	0.859	0.745	0.633
1992	0.889	0.691	0.584

also more movement in the population as its members are forced to spend more time and cover greater distances in searching for prey. That this scenario is consistent with the observations in no way implies that it is the only one possible, or is the actual cause of the observed changes. For example, the surveys are carried out at essentially the same time each year, but this does not necessarily imply that fish are at the same stage of some annual cycle (cf. the later spawning of capelin in recent years). In other words, the patterns observed for 1992, say, might be similar to those for 1985 had the 1985 survey been conducted later in the year.

In sum, an attempt to separate and estimate the spatial and temporal components of trawl-survey data has revealed some trends that coincide with the collapse of the northern cod stock and has permitted some conjecture as to the cause of these trends. The next step might be to construct mechanistic models to determine whether, indeed, the observed patterns can result from what is known about school structure and movement. Further work is required to determine the effects of movement on both design- and model-based estimates of abundance.

Acknowledgements

I would like to thank Pat Sullivan and two anonymous reviewers for their constructive comments and especially the reviewer whose sharp eyes prevented a couple of transcription errors in the mathematical expressions from going any further.

References

Aitchison, J., and Brown, J.A.C. 1957. The lognormal distribution. Cambridge University Press, Cambridge, U.K.

Anonymous. 1991. Report of the Workshop on the Applicability of Spatial Statistical Techniques to Acoustic Survey Data. Int. Counc. Explor. Sea C.M. 1991/D:40.

Brus, D.J., and de Gruijter, J.J. 1993. Design-based versus model-based estimates of spatial means: theory and application in environmental soil science. Environmetrics, **4**: 123–152.

Chakrabarti, M.C. 1962. Mathematics of design and analysis of experiments. Asia Publishing House, Bombay.

Cleveland, W.S. 1979. Robust locally weighted regression and smoothing scatterplots. J. Am. Stat. Assoc. **74**: 829–836.

Cochran, W.G. 1977. Sampling techniques. 3rd ed. John Wiley & Sons, Inc., New York.

Conan, G.Y. 1985. Assessment of shellfish stocks by geostatistical techniques. Int. Counc. Explor. Sea C.M. 1985/K:30.

Conan, G.Y., and Wade, E. 1989. Geostatistical analysis, mapping and global estimation of harvestable resources in a fishery of northern shrimp (*Pandalus borealis*). Int. Counc. Explor. Sea C.M. 1989/D:1.

Conan, G.Y., Buerkle, U., Wade, E., Chadwick, M., and Comeau, M. 1988*a*. Geostatistical analysis of spatial distribution of a school or herring. Int. Counc. Explor. Sea C.M. 1988/D:25.

Conan, G.Y., Moriashi, M., Wade, E., and Comeau, M. 1988*b*. Abundance and spatial distribution surveys of snow crab stocks by geostatistics. Int. Counc. Explor. Sea C.M. 1988/K:10.

Cressie, N.A.C. 1991. Statistics for spatial data. John Wiley & Sons, Inc., New York.

Francis, R.I.C.C. 1984. An adaptive strategy for stratified random trawl surveys. N.Z. J. Mar. Freshwater Res. **18**: 59–71.

Freire, J., Fernández, L., and González-Gurriarán, E. 1991. Spatial distribution of decapod crustaceans in the Galician continental shelf (NW Spain) using geostatistical analysis. Int. Counc. Explor. Sea C.M.1991/K:4.

González-Gurriarán, E., Freire, J., and Fernández, L. 1993. Geostatistical analysis of spatial distribution of *Liocarcinus depurator, Macropipus tuberculatus* and *Polybius henslowii* (Crustacea:Brachyura) of the Galician continental shelf (NW Spain). Mar. Biol. **115**: 453–461.

Guillard, J., Gerdeaux, D., and Chautrin, J.M. 1990. The use of geostatistics for abundance estimation by echointegration in lakes: the example of Lake Annecy. Rapp. P.-v. Réun. Cons. Int. Exlpor. Mer, **189**: 410–414.

Kamat, A.R. 1953. On the mean successive difference and its ratio to the root mean square. Biometrika, **40**: 116–127.

Pennington, M. 1983. Efficient estimators of abundance for fish and plankton surveys. Biometrics, **39**: 281–286.

Petitgas, P. 1993. Geostatistics for fish stock assessments: a review and an acoustic application. ICES J. Mar. Sci. **50**: 285–298.

Petitgas, P., and Poulard, J.C. 1989. Applying stationary geostatistics to fisheries: a study on hake in the Bay of Biscay. Int. Counc. Explor. Sea C.M. 1989/G:62.

Simard, Y., Legendre, P., Lavoie, G., and Marcotte, D. 1992. Mapping, estimation biomass, and optimizing sampling programs for spatially autocorrelated data: case study of the northern shrimp (*Pandalus borealis*). Can. J. Fish. Aquat. Sci. **49**: 32–45.

Simard, Y., Marcotte, D., and Bourgault, G. 1993. Exploration of geostatistical methods for mapping and estimating acoustic biomass of pelagic fish in the Gulf of St. Lawrence: size of echo-integration unit and auxiliary environmental variables. Aquat. Living Resour. **6**: 185–199.

Sullivan, P.J. 1991. Stock abundance estimation using depth-dependent trends and spatially correlated variation. Can. J. Fish. Aquat. Sci. **48**: 1691–1703.

Warren, W.G. 1994. The effect of fish movement on trawl survey estimates of abundance: the northern cod. Int. Counc. Explor. Sea C.M. 1994/D:9.

© 1997 NRC Canada

Environmental analysis of Atlantic cod (*Gadus morhua*) migration in relation to the seasonal variations on the Northeast Newfoundland Shelf

E. Colbourne, B. deYoung and G. A. Rose

Abstract: Comparison of historical (1930–1989) and recent (1990–1993) oceanographic data from the Northeast Newfoundland Shelf reveals a significant phase lag in the normal seasonal cycle of temperature and salinity. Atlantic cod (*Gadus morhua*) migrating along hypothesized circular routes during the early 1990s experienced temperatures up to 1.0°C below average, particularly at depths typical of the inshore cod fishery. Cod likely spent up to three times longer in subzero °C water during the early 1990s than was typical for the years 1930–1989. The time spent in subzero °C water during normal and warm years was relatively independent of timing of the migration, but even a delay of 1 mo during the early 1990s put cod in subzero °C water twice as long as normal. In contrast, no net salinity anomaly was experienced along the tracks. Temperatures experienced by cod along migration routes have a much larger range and a mean value up to 1.0°C higher than the vertically averaged temperatures at Station 27. In addition, the interannual average temperature along the migration routes, while exhibiting similar trends, was up to an order of magnitude higher (≈3.0 versus ≈0.3°C) than the vertically averaged temperatures obtained from a fixed point on the shelf (Station 27).

Résumé : La comparaison de données océanographiques anciennes (1930–1989) et récentes (1990–1993) pour la partie nord-est de la plate-forme de Terre-Neuve révèle un déphasage important dans le cycle saisonnier normal de la température et de la salinité. Les morues (*Gadus morhua*) qui, au début des années 90, empruntaient les voies de migration circulaires qu'on leur attribue ont été soumises à des températures qui tombaient jusqu'à 1,0°C au-dessous de la moyenne, particulièrement aux profondeurs auxquelles se pratique la pêche côtière à la morue. Les morues ont probablement passé jusqu'à trois fois plus de temps dans des eaux à moins de 0°C au début des années 90 que dans les années 1930 à 1989. Le temps passé dans des eaux à moins de 0°C au cours des années normales et chaudes était relativement indépendant de l'époque de la migration; mais, au début des années 90, un retard de 1 mo seulement obligeait les morues à passer deux fois plus de temps que d'habitude dans des eaux à moins de 0°C. Par contraste, aucune anomalie nette de la salinité n'a été observée le long des voies. Les températures auxquelles sont soumises les morues le long des voies de migration s'étendent sur une plage beaucoup plus large que les températures mesurées sur la verticale à la Station 27, et leur valeur moyenne est plus élevée, l'écart pouvant atteindre 1,0°C. De plus, la température moyenne le long des voies de migration, calculée sur plusieurs années, présentait des tendances similaires mais était plus élevée d'un ordre de grandeur (≈3,0 par rapport à ≈0,3°C) que la moyenne des températures mesurées sur la verticale en un point fixe sur la plate-forme (Station 27).
[Traduit par la Rédaction]

Introduction

Recent studies have suggested that environmental conditions (temperature, salinity, currents, etc.) on the continental shelf of Atlantic Canada may influence the distribution, recruitment, migration, and behaviour of migrating fish such as northern cod (*Gadus morhua*) (deYoung and Rose 1993; Myers et al. 1993; Rose et al. 1994; Taggart et al. 1994). A common approach in such studies is to relate different indices of fish biology, such as biomass, recruitment, growth, or condition factors, to time series of environmental indices, such as volume or area of subzero °C water, bottom temperatures, or vertically averaged temperature or salinity obtained from observations made at some fixed point like Station 27 (Fig. 1). Although there is high spatial coherence between the temperatures at Station 27 and across the shelf over the same depth range (Petrie et al. 1991; deYoung et al. 1994), this approach assumes that station conditions mimic the environment experienced by cod during seasonal migrations from the deep waters offshore to the inshore bays along Newfoundland.

During the Northern Cod Science Program (NCSP) and the Ocean Production Enhancement Network (OPEN), oceano-

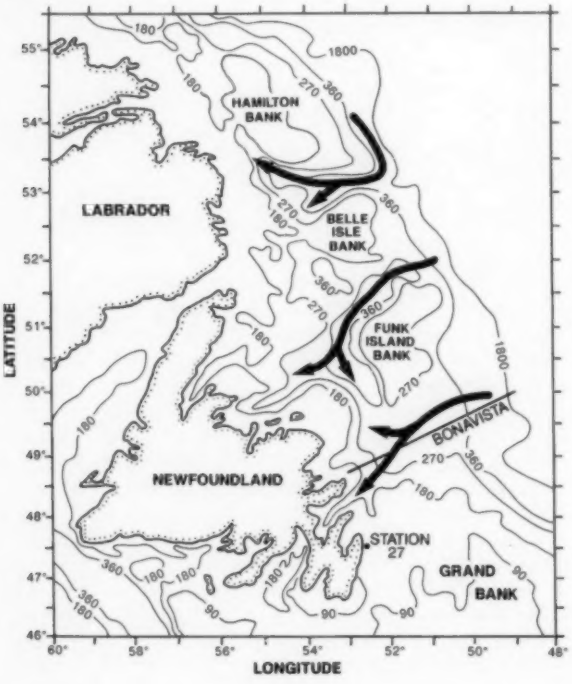
Received April 6, 1995. Accepted November 30, 1995.
J13309

E. Colbourne and G.A. Rose.[1] Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.
B. deYoung. Physics Department, Memorial University of Newfoundland, St. John's, NF A1B 3X7, Canada.

[1] Present address: Fisheries and Marine Institute, Memorial University of Newfoundland, St. John's, NF A1C 5R3, Canada.

© 1997 NRC Canada

Fig. 1. Location map of the study area showing the positions of the standard Bonavista transect, Station 27, and the cod migration routes predicted by Rose (1993). Isobaths are in metres. Redrawn from Rose (1993).



graphic surveys were carried out at approximately monthly intervals on the Northeast Newfoundland Shelf from early May to November from 1990 to 1993. These data, combined with oceanographic observations made during fisheries research and assessment surveys, have made it possible to resolve the seasonal cycles in the oceanographic environment during the early 1990s over large spatial areas on the Northeast Newfoundland Shelf. As a result, a more realistic approach to ecosystem research is possible, particularly as it pertains to migrating fish such as northern cod. From 1930 to 1989, an extensive temperature and salinity data set available from the Marine Environmental Data Service (MEDS) in Ottawa, Canada, and from archives at the Northwest Atlantic Fisheries Center (NAFC) readily establishes the long-term mean seasonal cycle (Colbourne et al. 1994; deYoung et al. 1994).

Tagging studies, biological indicators, and data from the commercial fishery have been used to describe general patterns of the migrations of cod from the offshore areas of the continental shelf to the inshore feeding grounds (Templeman 1966; Lear 1984). Tagging studies carried out over several decades support the existence of migratory circuits that are to a large extent spatially repeated from year to year (Templeman 1979; Lear 1984; Rose 1993; Taggart et al. 1995). More recently, combined acoustic tracking and tagging studies have identified specific migration corridors wherein cod move from the offshore to inshore areas along deep cross-shelf trenches that transect the continental shelf (Rose 1993; Rose et al. 1995). These corridors are probably used by cod because, being deeper, their bottom waters are warmer because the topography "cuts through" the three-dimensional temperature field. These various data have been used to define the approximate spatial extent of migrating cod throughout a full seasonal cycle.

We infer a circular migratory circuit from the offshore to inshore areas in the south, then north along the east and northeast coast of Newfoundland to southern Labrador, and eventually offshore to deeper water during the autumn where overwintering occurs along the edge of the continental shelf, as suggested by Rose (1993). We also examined other smaller scale migratory circuits from the shelf edge in spring through the Bonavista migration corridor (southern most route, Fig. 1) to the bays along the Avalon Peninsula and offshore along the same path during autumn.

The aim of this paper is to review the seasonal character of the oceanography on the Newfoundland Shelf during the period 1990–1993, with specific reference to the long-term mean, and to investigate the potential effects of oceanographic conditions on migrating cod. We develop a cod migration model utilizing both recent and historical oceanographic data sets to simulate the environmental conditions cod experience as they move along their migration routes. The representativeness of data from a fixed point on the continental shelf, specifically Station 27, to conditions along the simulated migration tracks is also evaluated.

Methods

Station 27 is one of the most frequently monitored hydrographic stations in the Northwest Atlantic Ocean. Data collected at this site have been used in several environmental monitoring and ocean climatic studies (e.g., Petrie et al. 1992; Colbourne et al. 1994; Drinkwater 1994). The position and frequency of occupation of this station make it well suited for determining the phase and amplitude of the seasonal cycle in temperature and salinity in the inshore branch of the Labrador Current in both the upper layer and the center of the cold intermediate layer (CIL) (Petrie et al. 1991; Colbourne et al. 1994).

Following the general methods of Smith (1983), Petrie et al. (1991), and Myers et al. (1990) and detailed descriptions in Colbourne et al. (1994) and Colbourne and Fitzpatrick (1994) the seasonal cycle in the temperature and salinity fields at selected water depths was determined by fitting a least-squares regression of the form $\cos(\omega t - \phi)$ to the historical 1930–1989 and the 1990–1993 data sets, where ω is the frequency of the annual cycle and its harmonics, t is the time of the year, and ϕ is the phase. The two independent sets of regression coefficients were then used to calculate the seasonal cycles for temperature and salinity for the two time periods at depths typical of the inshore portion of the cod migration cycle.

While the Station 27 data set enables a temporal analysis of the oceanographic conditions at a fixed location on the Newfoundland Shelf, the standard Bonavista transect (Fig. 1; Anonymous, 1978), one of the most frequently monitored transects of the Labrador Current in the Northwest Atlantic, enables both a temporal and spatial analysis of oceanographic indices across the continental shelf (Colbourne and Senciall 1993). The historical (1930–1989) and the 1990–1993 data sets along this transect were quality controlled, linearly interpolated to 5.0-m depth intervals, and analyzed on a monthly basis. The area of subzero °C water (CIL) along the transect for each month was determined by projecting all temperature profiles within ±25′ of latitude of the standard Bonavista transect line onto a 5.0 km horizontal by 5.0 m vertical grid. The data were then averaged and the area inside the 0.0°C contour measured using a digital planimeter.

To examine the environmental conditions along cod migration routes, all data on the Newfoundland Shelf from 46 to 55°N latitude were grouped in the year ranges 1930–1989, 1977–1980, 1986–1988,

© 1997 NRC Canada

Fig. 2. Vertical cross-section of the summer (July–August) cold intermediate layer (CIL) of subzero °C water along the standard Bonavista transect for a warm year (1986), a cold year (1991), and the long-term mean (1930–1989).

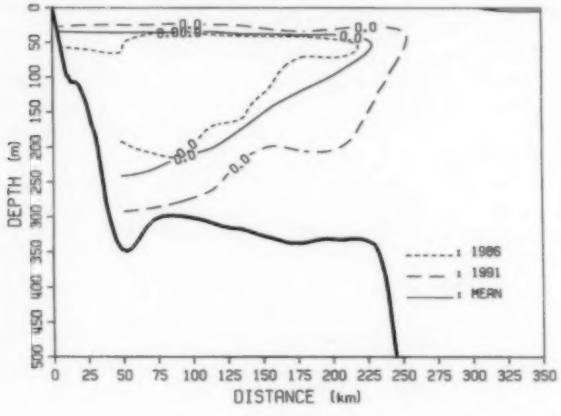
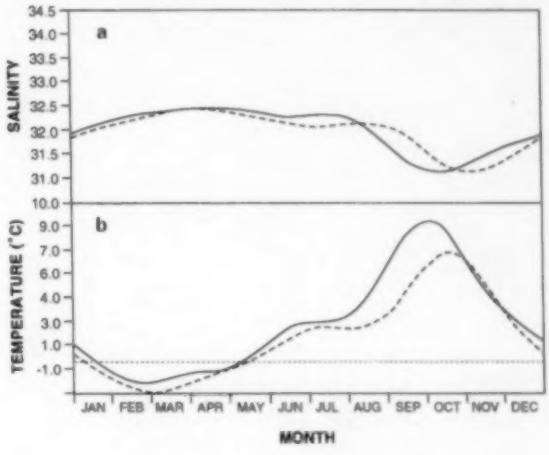


Fig. 3. Seasonal cycle of (*a*) salinity and (*b*) temperature at 30 m depth at Station 27 calculated from the least-squares regressions of all data from 1930–1989 (solid line) and 1990–1993 (broken line).



and 1990–1993 and then averaged into square projections of 0.25° latitude by 0.38° longitude and the mean for each month computed. Data were available at a sufficient number of grid points for each month for these years along the migration tracks used in our analysis, thus enabling the calculation of a temperature and salinity value at any time of the year on the shelf by linear interpolation in both space and time; any missing grid points were interpolated from nearest neighbours. A comprehensive analysis and description of the environmental data base in this area is found in deYoung et al. (1994), Colbourne and Senciall (1993), Colbourne and Fitzpatrick (1994), and Colbourne and Foote (1994). Once the temperature field $T(x,y,x,t)$ and salinity field, $S(x,y,z,t)$ (x and y are the horizontal spatial coordinates, z is the vertical or depth coordinate, and t corresponds to time of year) were known, the simulation of oceanographic conditions experienced by migrating fish was possible.

The simulations were performed by initiating the start time and position of the fish in the spring along the edge of the continental shelf off Cape Bonavista. The fish were then moved along migration routes near the bottom towards the coast through the Bonavista migration corridor at a constant speed. After the fish arrived inshore, they were allowed to either move northward along the coast at a constant depth or remain in the same general area until autumn, after which they moved offshore along the bottom to the edge of the shelf (see Fig. 5*b*). As the fish moved through both time and space the temperature and salinity values they experienced were calculated using the linear model described above.

Seasonal oceanography

The dominant feature of the temperature structure on the continental shelf throughout most of the year, except the winter months when the thermal stratification breaks down, is the large volume of subzero °C water trapped between warmer surface and bottom continental slope water, commonly referred to as the cold intermediate layer (CIL) (Petrie et al. 1988). The summer (July–August) CIL bounded by the 0.0°C isotherm shows significant variability from the mean in the offshore extent, maximum depth, and cross-sectional area between a warm year (1986) and a cold year (1991) (Fig. 2). A discussion of the interannual variability of various CIL indices is presented in Colbourne et al. (1994) and Colbourne and Senciall (1993). Subzero °C water occupies a significant portion of the total volume of water on the continental shelf, with subzero °C water always present from the bottom of the seasonally heated upper layer (30–50 m in summer) to the bottom nearshore (depths >50 m) to about 50 km offshore (depths >250 m) depending on local bathymetry.

The seasonal cycles in the temperature and salinity fields on the Newfoundland Shelf were first investigated by Bailey (1961) and modeled by Petrie et al. (1991). As described earlier, we fitted harmonic regressions to the recent (1990–1993) and historical (1930–1989) data sets. This analysis allowed us to investigate in detail the effect of cold years on the phase and amplitude of the seasonal cycles and the possible implications for the fishery.

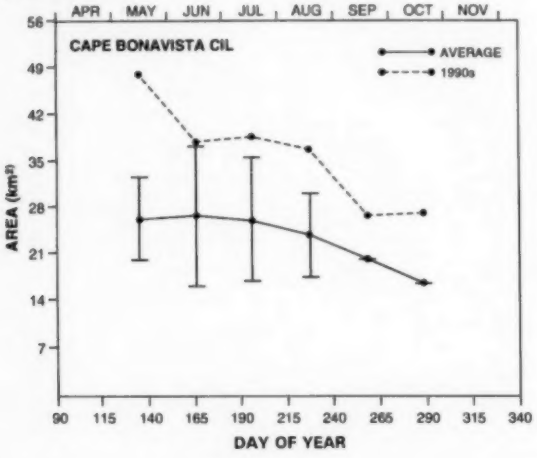
Winter and spring salinities at Station 27 during the early 1990s were near normal at 30 m depth, below normal by about 0.25 psu during late spring and early summer, and up to 0.5 psu above normal from midsummer to early autumn (Fig. 3*a*). These anomalies were likely the result of a delayed upstream runoff and ice melt during the spring. Surface salinity normally reaches a minimum at Station 27 in late September (Myers et al. 1990), but this minimum was not observed until early November during the period 1990–1993, up to 5 wk later than normal.

During the winter months of the early 1990s the 30 m depth temperature was up to 0.5°C below normal and up to 3.0°C below normal during the summer and early autumn. By late October, temperatures rebounded and were near the long-term average for the remainder of the year (Fig. 3*b*). The amplitude of the seasonal temperature cycle which normally reaches its maximum by late September was delayed by up to 3–4 wk during the early 1990s. These observed phase shifts in both the temperature and salinity seasonal cycles were the result of anomalously cold air temperatures (Findlay and Deptuch-Stapf 1991), above-normal spring ice coverage, and delayed ice melt experienced on the Newfoundland Shelf since the late 1980s to 1993 (Prinsenberg et al. 1997).

The seasonal variation in the area of the CIL for the two time periods shows a relatively constant area of subzero °C

© 1997 NRC Canada

Fig. 4. Seasonal variation in the cold intermediate layer (CIL) of subzero °C water along the Bonavista transect based on all data from 1930–1989 (solid line) and 1990–1993 (broken line). Vertical bars represent SD.



water along the Bonavista transect from May to July after which it shows a gradual decrease during early autumn, reaching its minimum by November after which it increases again due to the onset of winter cooling (Fig. 4). During the early 1990s, this area was significantly larger (by 30–40%) than the long-term average. It is clear from this analysis that the oceanographic conditions on the Newfoundland Shelf during the early 1990s were anomalous in both amplitude and phase.

Cod migration

Historically the northern cod stock was believed to consist of several overlapping and intermingling populations over an area from the northern Grand Banks to northern Labrador (Harris 1990). These populations undertook seasonal migrations from the warmer slope water offshore to the inshore areas and bays along the coast of Newfoundland and Labrador during spring and summer to feed on mainly caplin (*Mallotus villosus*), a species also undergoing an annual migration (Lear and Green 1984). The southernmost cod migration route observed by Rose (1993) through the Bonavista corridor between the northern Grand Bank and southern Funk Island Bank (Fig. 1) was the target of intensive cod migration and oceanographic studies in the springs of 1990, 1991, and 1992 (Rose 1993; Rose et al. 1995; DeBlois and Rose 1995). In addition, under the NCSP, this route was monitored at approximately monthly intervals during spring and summer of 1992 and 1993 to resolve the seasonal variations in the oceanographic conditions.

During the studies of the Bonavista corridor, cod were tracked acoustically along the route for up to 36 d (Rose et al. 1995). Up to 6500 cod were tagged from the migrating aggregations each year (G.A. Rose, unpublished data). The general patterns of tag returns during 1990 and 1991 (a moratorium was declared on fishing in July 1992; hence, tag returns declined to near nil) were described by Rose (1993). Here, we repeat details essential to the present study. Tags were returned from the inshore regions along the Avalon Peninsula and the east coast of Newfoundland during July and along the northeast Newfoundland coast to St. Anthony during August. Later returns were received from southern Labrador to September and near the edge of the shelf the following winter (Fig. 5*a*). The pattern is suggestive of a circular migration cycle from the offshore to inshore in the spring, north along the coast during summer, and offshore during late autumn (Fig. 5*b*). We infer that this route approximates the maximum range of migrating cod during recent years. In keeping with the south–north movement patterns over a longer time period, Chen et al. (1994) used the inshore commercial cod landings between 1974 and 1991 to show a spatial pattern in the timing of the inshore fishery, with the fishery starting along the Avalon Peninsula in late June but not until August in southern Labrador.

In this study, we used the circular routes (Fig. 5*b*) to examine the oceanographic conditions experienced by fish as they undertook their seasonal migrations. However, we emphasize that other more northerly migration routes (Fig. 1) lead directly to the northerly inshore zones and may have been the chief migration routes of some cod in former years. Nevertheless, the southernmost route was utilized by the bulk of northern cod in the early 1990s during their inshore migrations, and the circular route we used was supported by tagging from 1990 to 1992 and hence is the most reliable circuit upon which to base our initial simulations.

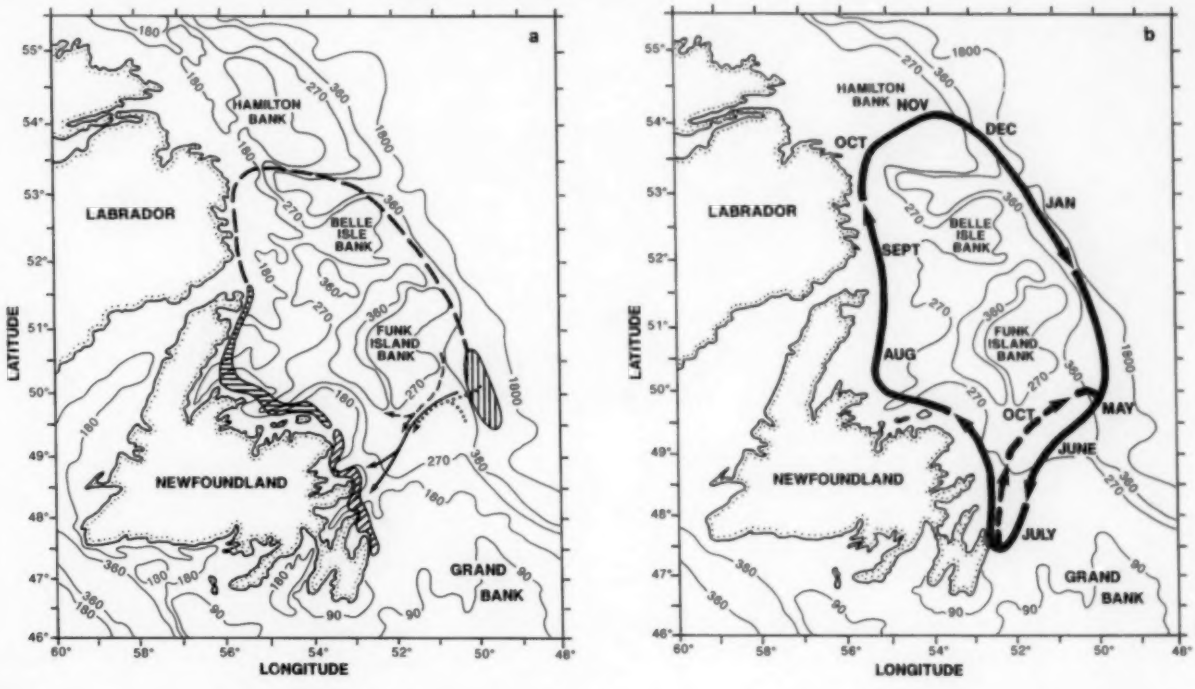
The basic assumptions we used in our simulations were that cod migrate along the routes near the bottom across the shelf into shallower water near the coast. The along-shore summer migration was fixed at a constant 30 m depth. This depth was chosen to correspond to the approximate median depth of the inshore commercial cod trap fishery. The average migration speeds along the cross-shelf (spring) leg and the inshore northward (summer) leg were fixed at about 8 km/d and about 5 km/d during the autumn offshore migrations. These speeds were necessary to match the timing of the tag returns and the timing of the inshore commercial fishery and are within the range of the groundspeeds observed acoustically on the cross-shelf leg during spring. The mean groundspeed observed during the acoustic tracking experiments of 1992 was about 9 km/d and the average during all three years ranged from 7 to 24 km/d. A detailed analysis of these cod migration speeds in relation to ambient currents on the Northeast Newfoundland Shelf is given in Rose et al. (1995).

Results

To examine the oceanographic conditions cod experience on their migration routes, we started the model simulations in mid-May near the edge of the continental shelf off Cape Bonavista at the seaward end of the Bonavista migration corridor. To evaluate the sensitivity of the timing of the migration cycle to the oceanographic conditions, we also ran simulations starting in mid-April and mid-June. Fish migrating shoreward along the external route (Fig. 5*b*), starting in mid May, through the Bonavista corridor in water depths ranging from 500 to 1000 m experience average (1930–1989) temperatures decreasing from about 3.5°C near the shelf edge to 2.0°C near the center of the corridor and to –1.0°C as they move onto the Grand Bank in about 100–200 m depth (Fig. 6). Temperatures

© 1997 NRC Canada

Fig. 5. (*a*) Migration patterns of northern cod observed in June and July (solid line, 1990; broken line, 1991; dotted line, 1992). Hatching indicates areas of inshore tag returns in July (diagonal hatching), August (horizontal hatching), and the following winter (vertical hatching). The heavy broken line indicates the boundary of the migration route indicated by Rose (1993). Adapted from Rose (1993). (*b*) Migration routes considered in this study showing the timing of the migration. Bathymetry in metres.

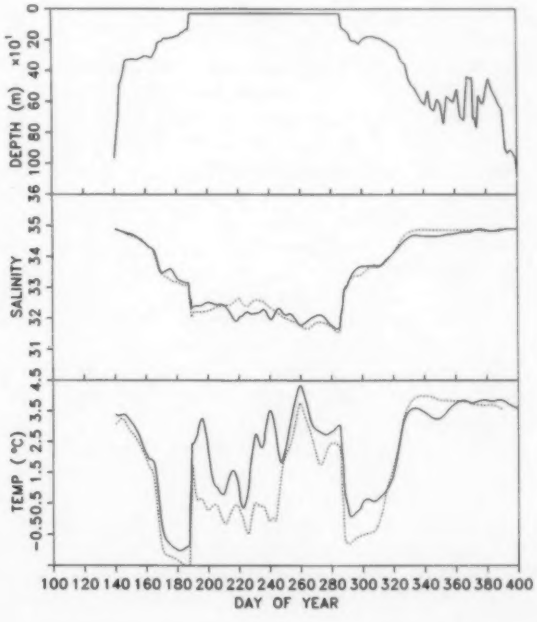


rise again as the cod move into shallower water near the coast and into the bays, decrease as they migrate northward along the coast during early July, and increase as they move north to southern Labrador from early August through to September. By early autumn the seasonal warming reaches its maximum near bottom in water depths typical of the inshore cod trap fishery. From late September to early October the fish begin to move offshore across Hamilton Bank in roughly 0.0°C water which then increases to between 3.0 and 4.0°C as they move along the shelf edge during the winter months. Cod migrating along this route experience an average temperature of 2.0°C throughout the year.

Similarly, the average salinity decreases from about 34.8 psu in the deep water at the shelf edge to 33.0 psu on the Grand Bank to 32.3 psu near the coast in water depths of about 30 m. The salinity then gradually decreases from south to north from about 32.3 psu along the Avalon Peninsula to about 31.7 psu off southern Labrador and increases again to near 34.8 psu along the shelf break.

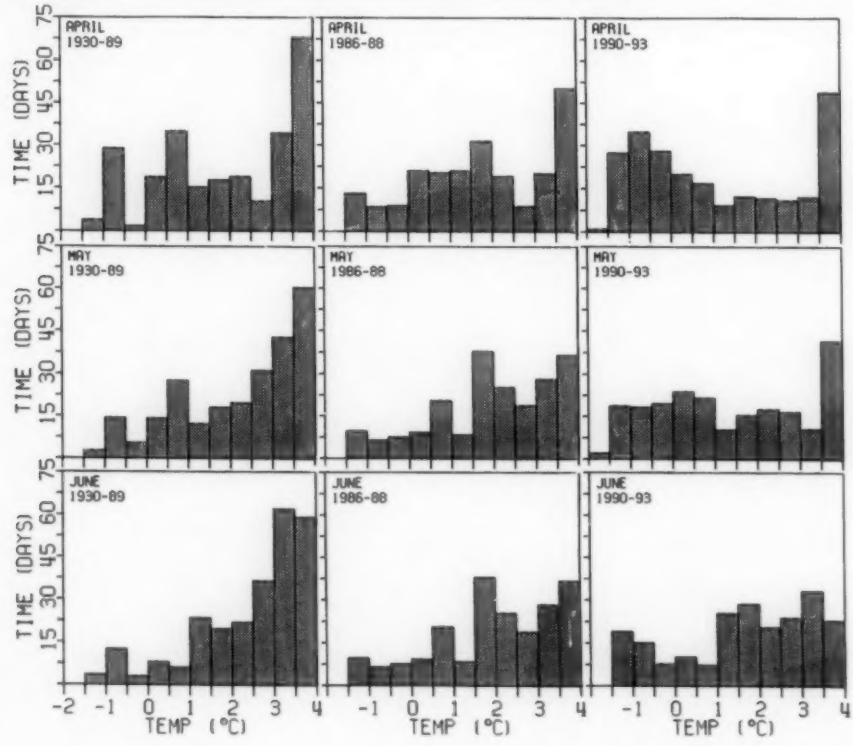
During the period 1990–1993, cod experienced slightly below-normal temperatures along the edge of the continental shelf in water depths below 300 m and in the deep trench along the Bonavista migration corridor. Significant negative temperature anomalies ranging from 0.5 to 1.0°C below normal were experienced across the Grand Bank and Hamilton Bank and from 1.0 to 3.0°C below normal along the coast of Newfoundland and Labrador in water depths typical of the inshore cod trap fishery (Fig. 6). During this period, migrating cod experienced an average temperature of 1.1°C, about

Fig. 6. Depth, salinity, and temperature encountered by cod as they migrate along the external migration route shown in Fig. 5*b* based on all data from 1930–1989 (solid line) and 1990–1993 (broken line).



© 1997 NRC Canada

Fig. 7. Histograms of the time that cod occupied various temperature ranges along the migration route for migration start times of April, May, and June based on the average of all available data from 1930–1989, 1986–1988, and 1990–1993.



1.0°C below the 1930–1989 average. Salinities during the same period showed no significant departures from normal in the offshore regions but fluctuated by about 0.3 psu above and below the mean in the inshore regions.

The environmental conditions experienced by migrating cod along tracks over smaller spatial scales show very similar trends. However, the inshore portion of the time series has a higher mean temperature corresponding to the latitudinal gradient in the summer temperature in the inshore regions of the continental shelf (Colbourne and Foote 1994). For example, if cod started their migration at the edge of the continental shelf in May (Fig. 5*b*) and moved inshore through the Bonavista corridor to the Avalon Peninsula by July, staying inshore at approximately the same latitude until September and then finally migrating offshore along a similar path during autumn, they would encounter an average temperature of 5.2°C in the inshore region compared with 2.3°C along the inshore portion of the external migration route discussed above.

The large volume of subzero °C water that is present year-round on the Northeast Newfoundland Shelf, even during warm years (Fig. 2), forces fish migrating along or near the bottom from the offshore to the inshore to transit approximately 30 km of subzero °C water, even more during cold years. As a result the time that migrating fish spend in various temperature ranges along their routes depends on the environmental conditions (e.g., average 1930–1989, warm 1977–1980 and 1986–1988, and cold 1990–1993 periods) as well as their migration start times (Fig. 7). The migration start times simulated here (April, May, and June) refer to the month cod started their shoreward migration leg from the edge of the continental shelf. For a start time in May, on average, cod would spend up to 60% of their time in water from 2.0 to 4.0°C during average and warm years but only about 40% during the cold period of the early 1990s and the remainder of the time in colderwater.

For average (1930–1989) and warm (1977–1980 and 1986–1988) periods, with normal migration start time (May), cod would spend about 8% of their time in water below 0.0°C compared with 21% during the cold years of the early 1990s, almost three times longer than normal (Fig. 8). If migration had been delayed by one month during the 1990s the time in subzero °C water, although reduced would still have been greater than average by a factor of two. During warm years, time spent in subzero °C water is almost independent of migration delay times from April to June.

In general, the percentage of time migrating fish would occupy various salinity ranges during average and cold periods shows a somewhat different distribution (at a salinity bin resolution of 0.5 psu); however, there was little difference in the total time spent in high-salinity water (>33.0 psu), about 65%, and low-salinity water (<33.0 psu), about 35% (Fig. 9). The difference in the distributions in the salinity range of 32.5–33.0 psu is the result of the higher than normal salinity experienced in August and September in the inshore region (water depths from 0 to 50 m) during the period 1990–1993 (Figs. 3*a* and 6).

© 1997 NRC Canada

Fig. 8. Histograms of the percentage of time cod spent in subzero °C water for migration start times of April, May, and June for average conditions (1930–1989), cold conditions (1990–1993), and two warm periods (1977–1980 and 1986–1988).

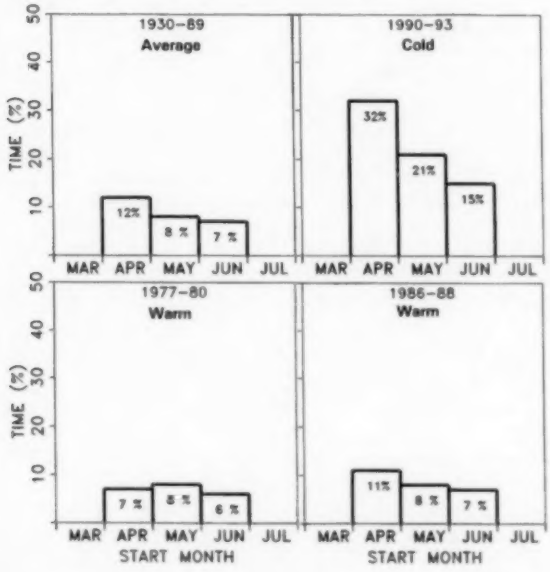
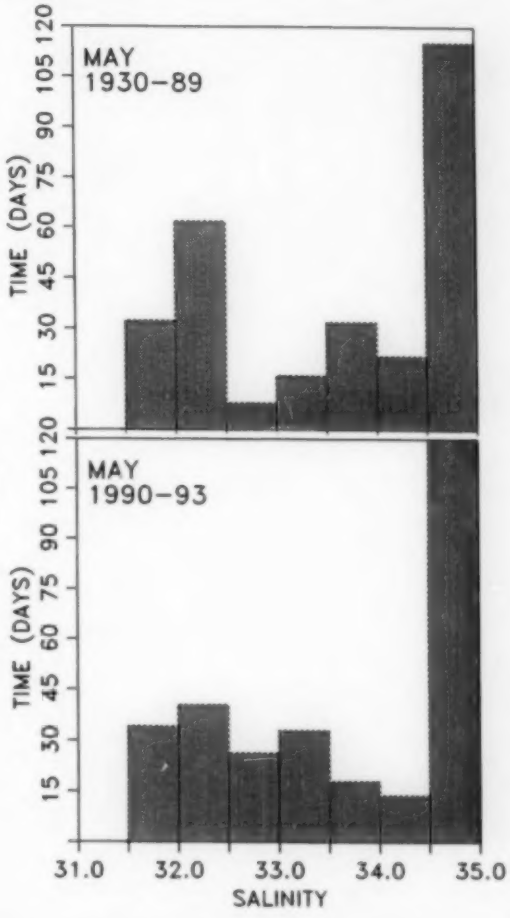


Fig. 9. Histograms of the time that cod occupied various salinity ranges along the migration route for a migration start time in May based on the average of all available data from 1930–1989 and 1990–1993.



Comparison with static conditions

As shown, cod migrating from offshore (water depths >500 m) to the inshore regions (depths ≈30 m) typically encounter temperatures ranging from >3.0°C in deep water and along the coast to between 0.0 and –1.5°C in the depth range from approximately 50 to 100 m depth nearshore and on the banks. How does a time series of fish–temperature (the water temperature experienced by moving fish) over this depth range differ from a time series obtained at a single point (e.g., Station 27, Fig. 1) on the continental shelf? Since migrating fish integrate the ocean environment over significant depth ranges, vertically averaged data probably represents, the best overall measure from a fixed point with which to evaluate oceanographic influences in general. A comparison of the annual vertically averaged (0–176 m) Station 27 temperature and the fish–temperature (along the external migration path presented in Fig. 5*b*) time series shows different trends and ranges over the same time period (Fig. 10*a*). The mean vertically averaged temperature at Station 27 from mid-May to December during 1991 was –0.1°C compared with 1.1°C along the migration track for the same time period. The temperature at Station 27 ranged from –1.7 to 1.8°C, and along the migration track, during the same period, the temperature ranged from –1.5 to 3.8°C. Thus for a given year, migrating fish experience a much greater range and higher mean temperature than that indicated by the vertically averaged Station 27 data.

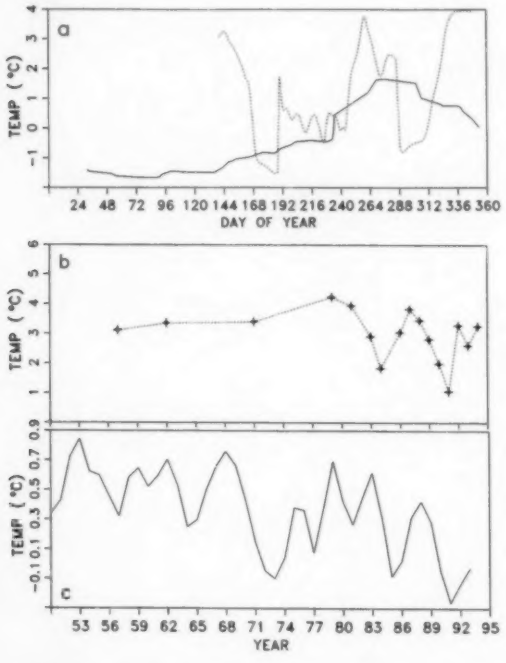
To examine interannual variability in migration path temperatures the small-scale migration path (Fig. 5*b*) offered the best data coverage. Even in this case, it was necessary to group the historical data, particularly for earlier periods, to obtain adequate spatial coverage throughout the year. Thus the fish temperatures are for 1955–1959, 1960–1964, 1970–1972, 1979–1980, 1981, 1983, 1984, 1986, 1987, 1988, 1989, 1990, 1991, 1992, 1993, and 1994. The annual average fish temperatures (Fig. 10*b*) along this path are higher than the mean temperature along the external route shown in Fig. 5*b* and the vertically averaged Station 27 temperature (Fig. 10*c*). The two time series show similar interannual variations, corresponding to periods of colder than normal conditions (Colbourne et al. 1994, 1997). However, the vertically averaged Station 27 time series has a much smaller range, and the amplitude in a given year, such as 1991, differs by as much as 1.0°C. Additionally, we find that the long-term average fish temperature is greater than the vertically averaged Station 27 temperature by an order of magnitude, a large and potentially significant difference, especially for applications involving cod growth models.

Discussion

Recent tagging, acoustic tracking, and the commercial inshore landings data indicate that northern cod generally follow circular migration routes from wintering areas near the

© 1997 NRC Canada

Fig. 10. (*a*) Vertically averaged temperature at Station 27 during 1991 (solid line) and the temperature cod encountered during the season along the external migration route shown in Fig. 5*b* during the early 1990s (broken line); (*b*) average annual temperature encountered by cod along the southern small-scale migration route shown in Fig. 5*b*; the crosses are centered at the time period of data availability; (*c*) time series of the annual vertically averaged Station 27 temperature.



edge of the continental shelf shoreward through the deep cross-shelf trenches containing warm slope water. The large-scale migration route chosen for investigation in this paper is based on these data and is intended to represent the maximum areal migration of the southern component of northern cod (Rose 1993). Other migration routes no doubt are possible, particularly for the historical stock which was much larger in numbers and covered a much greater geographical area (deYoung and Rose 1993). In keeping with this interpretation, Wroblewski et al. (1995) have shown that cod move along the shelf edge northward and southward between Hamilton Bank and the Grand Bank in the winter prior to spawning. Nevertheless, we believe that the routes we have used are sufficiently realistic to allow us to compare oceanographic conditions experienced by migrating fish during different climatic periods. Our results indicate that cod migrating along these routes during the early 1990s experienced significant negative temperature anomalies, particularly in the inshore region at depths typical of the inshore fishery.

The delay in the normal seasonal cycle during the 1990s may have affected the normal migration and spawning patterns of northern cod and could have been responsible for a redistribution of the stocks. Rose (1993) observed delays in spawning and migration inshore along the Bonavista corridor, especially in 1991 and 1992. In keeping with these delays, the inshore fishery began several weeks later in the early 1990s than was historically typical. In particular, Chen et al. (1994) showed that in 1991, which was characterized by very cold conditions, the delays in the onset of the inshore fishery were the longest ever observed. Additionally, the normal migration and spawning of caplin, the chief prey of cod, to the beaches along the east coast of Newfoundland had been delayed by up to 1 mo since 1991 (Nakashima and Winters 1995; J. Carscadden, Department of Fisheries and Oceans, St. John's, NF A1C 5X1, personal communication). This is consistent with the observed phase shift in the normal seasonal temperature cycle reported here. Our results also show that the time fish spent in very cold water (<0.0°C) along the migration path during the 1990s would have been significantly reduced by delaying their onshore migration by 1 mo. We suggest that the confounding influences of a poor environment and a disrupted food supply (mainly caplin) contributed to recent observed changes in northern cod migration and distribution.

The effects of severe environmental conditions on the general condition and behaviour of cod warrant further comment. During the period 1990–1993, cod had approximately 35% less heat available along their migration routes relative to 0.0°C than during average conditions from 1930 to 1989. Resultant reductions in metabolic rates due to the decline in water temperature integrated along migration tracks coupled with a decreased food supply could have caused delays in the attainment of peak prespawning condition normally reached during late autumn (Taggart et al. 1994). Consequently, the timing of spawning and post-spawning migrations may have been affected. Such reactions to cold are consistent with the delayed spawning and the general southerly shift in spawning aggregations observed during the early 1990s (deYoung and Rose 1993).

To conclude, this work presents a first attempt to quantify at large spatial and temporal scales the oceanographic conditions that cod are likely to experience along their seasonal migration routes from offshore to the shores around Newfoundland. Our results may be useful particularly in relation to cod growth models and condition studies, as they provide biologically relevant time series of temperatures experienced by migrating cod.

Acknowledgements

We thank the technical staff (C. Fitzpatrick, P. Stead, and J. Walpert) of the Northwest Atlantic Fisheries Center (NAFC) for the professional work in collecting and processing data. We also thank D. Arenillas and D. Senciall for computer software support and the many scientists at the Department of Fisheries and Oceans for collecting and providing much of the data contained in this analysis and the Marine Environmental Data Service (MEDS) in Ottawa for providing most of the historical data. We thank Drs. J. Helbig and L. Dickie for reviewing and providing helpful comments on this manuscript. This work was funded by the Northern Cod Science Program (NCSP) of the Department of Fisheries and Oceans and the Ocean Production Enhancement Network (OPEN).

References

Anonymous. 1978. List of ICNAF standard oceanographic sections and stations. ICNAF Selected Pap. No. 3.

© 1997 NRC Canada

Bailey, W.B. 1961. Annual variations of the temperature and salinity in the Grand Banks region. Fish. Res. Board Can. MS Rep. Ser. No. 74.

Chen, X.H., Shelton, P.A., and Bath, A.J. 1994. Relationships between temperature and landing patterns in the southern Labrador and eastern Newfoundland inshore cod fishery. Fish. Oceanogr. **3**: 191–196.

Colbourne, E.B., and Fitzpatrick, C. 1994. Temperature, salinity and density at Station 27 from 1978 to 1993. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 159.

Colbourne, E.B., and Foote, K.D. 1994. Spatial temperature and salinity fields over the shelves of Newfoundland and Labrador. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 160.

Colbourne, E.B., and Senciall, D. 1993. Temperature, salinity and density along the standard Bonavista Transect. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 150.

Colbourne, E.B., Narayanan, S., and Prinsenberg, S. 1994. Climatic change and environmental conditions in the Northwest Atlantic during the period 1970–1993. ICES Mar. Sci. Symp. **198**: 311–322.

Colbourne, E., deYoung, B., Naryanan, S., and Helbig, J. 1997. Comparison of hydrography and circulation on the Newfoundland Shelf during 1990–1993 with the long-term mean. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

DeBlois, E.M., and Rose, G.A. 1995. Effect of foraging activity on the shoal structure of cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **52**: 2377–2387.

deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. **50**: 2729–2741.

deYoung, B., Perry, F., and Greatbatch, R. 1994. Objective analysis of hydrographic data in the Northwest Atlantic. Can. Tech. Rep. Hydrogr. Ocean Sci. No. 130.

Drinkwater, K.F. 1994. Overview of environmental conditions in the Northwest Atlantic in 1993. NAFO SCR Doc. 94/20, Ser. No. N2385.

Findlay, B.F., and Deptuch-Stapf, A. 1991. Colder than normal temperatures over northeastern Canada during the 1980s. Clim. Perspect. Apr. Mon. Rev. **13**: 9–12.

Harris, L. 1990. Independent review of the state of the northern cod stock. Department of Fisheries and Oceans, Ottawa, Ont.

Lear, W.H. 1984. Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, as inferred from tagging studies. J. Northwest Atl. Fish. Sci. **5**: 143–159.

Lear, W.H., and Green, J.M. 1984. Migrations of the "northern" Atlantic cod and the mechanisms involved. In Mechanisms of migration in fishes. *Edited by* J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York. pp. 309–316.

Myers, R.A., Akenhead, S.A., and Drinkwater, K. 1990. The influence of Hudson Bay runoff and ice-melt on the salinity of the inner Newfoundland Shelf. Atmos.- Ocean, **28**: 120–157.

Myers, R.A., Drinkwater, K.F., Barrowman, N.J., and Baird, J.W. 1993. Salinity and recruitment of Atlantic cod (*Gadus morhua*) in the Newfoundland region. Can. J. Fish. Aquat. Sci. **50**: 1599–1609.

Nakashima, B.S., and Winters, G.H. 1995. Caplin in SA2 + Div. 3KL. DFO Atl. Fish. Res. Doc. 95/70, Chap. 5. pp. 72–80.

Petrie, B., Akenhead, S., Lazier, J., and Loder, J. 1988. The cold intermediate layer on the Labrador and Northeast Newfoundland shelves, 1978–1986. NAFO Sci. Counc. Stud. **12**: 57–69.

Petrie, B., Loder, J., Akenhead, S., and Lazier, J. 1991. Temperature and salinity variability on the eastern Newfoundland Shelf: the annual harmonic. Atmos.-Ocean, **29**:14–36.

Petrie, B., Loder, J., Lazier, J., and Akenhead, S. 1992. Temperature and salinity variability on the eastern Newfoundland Shelf: the residual field. Atmos.-Ocean, **30**: 120–157.

Prinsenberg, S.J., Peterson, I.K., Narayanan, S., and Omoh, J.U. 1997. Interaction between atmosphere, ice cover, and ocean off Labrador and Newfoundland from 1962 to 1992. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Rose, G.A. 1993. Cod spawning on a migration highway in the north-west Atlantic. Nature (Lond.), **366**: 458–461.

Rose, G.A., Atkinson, B.A., Baird, J., Bishop, C.A., and Kulka, D.W. 1994. Atlantic cod distributional changes and thermal variations in Newfoundland waters, 1980–1992. ICES Mar. Sci. Symp. **198**: 242–252.

Rose, G.A., deYoung, B., and Colbourne, E. 1995. Cod (*Gadus morhua*) migration speeds and transport relative to currents on the Northeast Newfoundland Shelf. ICES J. Mar. Sci. **52**: 903–913.

Smith, P.C. 1983. The mean and seasonal circulation off southwestern Nova Scotia. J. Phys. Oceanogr. **13**: 1034–1054.

Taggart, C., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment on the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

Taggart, C.T., Penny, P., Barrowman, N., and George, C. 1995. The 1954–1993 Newfoundland cod-tagging database: statistical summaries and spatial–temporal distributions. Can. Tech. Rep. Fish. Aquat. Sci. No. 2042.

Templeman, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Board Can. No. 154.

Templeman, W. 1979. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962–1966. ICNAF Res. Bull. **14**: 5–50.

Wroblewski, J.S., Kulka, D., Narayanan, S., Oake, A., Collier, A., and McGrath, B. 1995. Winter distribution and movement of northern Atlantic cod (*Gadus morhua*) along the Newfoundland–Labrador continental shelf edge derived from observations on commercial trawlers. Fish. Oceanogr. **4**: 128–146.

© 1997 NRC Canada

Spawning and year-class strength of northern cod (*Gadus morhua*) as measured by pelagic juvenile cod surveys, 1991–1994

John T. Anderson and Edgar L. Dalley

Abstract: Distribution and abundance of pelagic juvenile northern cod (*Gadus morhua*) were studied during four years following stock collapse. We nominally rank year-class strength as 1994 > 1993 ≥ 1992 > 1991. Pelagic juvenile cod were mostly absent within the inshore area in 1991 along the northeast coast of Newfoundland (NAFO 2J3KL) whereas in 1992–1994, cod were observed throughout the inshore. Offshore, cod were observed infrequently during 1991–1993. However, in 1994, a large concentration of cod was observed offshore on the Northeast Newfoundland Shelf. The offshore distributions reflect changes in the spawning distributions of adults. The inshore distributions are believed to reflect inshore spawning. Successful spawning was limited to 1–2 mo duration, although the spawning period differed among years. Larvae hatched primarily during August in 1992, July–August in 1993, and June in 1994. We estimate that spawning in 1994 occurred from late April through May, similar to the historical median spawning time, whereas spawning in 1992 and 1993 was late. The differences in spawning times are interpreted to reflect changing spawning behaviour by adults.

Résumé : Suite à l'effondrement des stocks, nous avons étudié pendant quatre ans la distribution et l'abondance des morues du Nord (*Gadus morhua*) juvéniles en phase pélagique. Nous classons les années selon l'effectif des classes de morues de la manière suivante: 1994 > 1993 ≥ 1992 > 1991. En 1991, les morues juvéniles pélagiques étaient essentiellement absentes de la zone côtière au nord-est de Terre-Neuve (divisions 2J3KL de l'OPANO), alors que de 1992 à 1994 les morues ont été observées partout dans la zone côtière. Au large des côtes, des morues n'ont été observées que rarement de 1991 à 1993. Cependant, en 1994, une grande concentration de morues a été observée au large sur la partie nord-est de la plate-forme de Terre-Neuve. La distribution des poissons au large reflète des changements dans la distribution des adultes lors de la fraye. La distribution des morues dans les eaux côtières semble correspondre à la situation de la fraye sur la côte. La période de ponte fructueuse était limitée à une durée de 1–2 mo, mais les dates variaient d'une année à l'autre. Les larves sont écloses principalement au mois d'août en 1992, en juillet et août en 1993 et au mois de juin en 1994. Nous estimons que la période de fraye, en 1994, s'est étendue de la fin d'avril à la fin de mai, ce qui correspond aux dates médianes établies historiquement, alors que la fraye a eu lieu plus tard en 1992 et 1993. On pense que les différences dans les dates de la période de fraye reflètent des changements dans le comportement génésique des adultes.
[Traduit par la Rédaction]

Introduction

The pelagic juvenile stage is a unique period in the life history of Atlantic cod (*Gadus morhua*). It occurs during the relatively short period following metamorphosis from the larval stage and prior to settlement to a demersal habitat in the autumn. Sampling populations of pelagic juvenile cod can provide important measurements of population dynamics relating to spawning and recruitment.

Geographic distributions of pelagic juvenile cod can delineate major nursery areas in relation to spawning populations (Riley and Parnell 1984; Sundby et al. 1989; Suthers and Frank 1989; Suthers and Sundby 1993). These distributions can vary significantly among years due to variations in ocean circulation affecting egg and larval drift which can significantly affect subsequent recruitment to the fishery in different stocks (Frank 1992; Polachek et al. 1992; Schopka 1994).

Population estimates of pelagic juvenile cod often predict recruitment (Campana et al. 1989; Sundby et al. 1989; Asthorsson et al. 1994; Jakupsstovu and Reinert 1994). These studies indicate that survival of a year-class is primarily determined during the egg and larval stages of cod. In addition, meaurements of age, growth histories, and biological condition of pelagic juvenile cod can provide important clues to factors influencing survival.

Historically, cod have spawned in offshore and inshore areas of Newfoundland and Labrador (Templeman 1981, 1989; Hutchings et al. 1994). However, the relative importance of inshore spawning compared with offshore has not been determined (Halliday and Pinhorn 1990; Hutchings et al. 1994; Anderson et al. 1995). Modelling studies of egg and larval drift suggest that eggs spawned on the shelf largely remain on the shelf, although downstream of their spawning sites (Helbig et al. 1992; Davidson and deYoung 1995). Some eggs and larvae may drift to the inshore, but this is predicted to be limited, except under specific

Received March 21, 1995. Accepted April 17, 1996.
J13448

J.T. Anderson and E.L. Dalley. Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

© 1997 NRC Canada

conditions of wind forcing. These drift predictions have been corroborated by field observations during the 1980's, a period in which spawning cod were distributed throughout the area and pelagic juvenile cod were found distributed extensively offshore and inshore (Anderson et al. 1995).

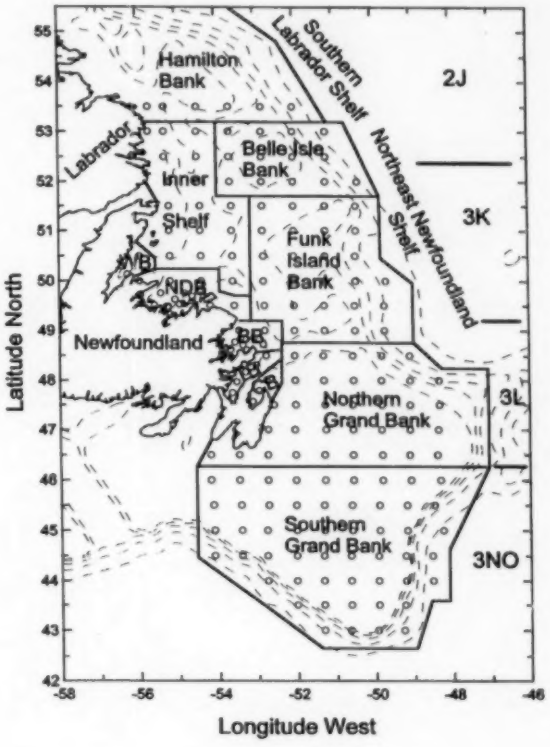
The spawning population of northern cod may shift its distribution south in response to changing ocean climate, cold temperatures in particular (deYoung and Rose 1993). A southward shift in spawning would affect the dispersal of eggs and larvae, possibly reducing survival. Similarly, when fish populations are significantly reduced due to overfishing, there may be changes in both the duration and timing of spawning (Hutchings and Myers 1993; Pedersen 1984) and the location where cod spawn (Rose et al. 1994; Kulka et al. 1995). Under these circumstances, we can expect changes in the geographic distribution, abundance, and age structure of pelagic juveniles.

The primary purpose of this study was to describe changes in the geographic distributions of pelagic juvenile cod following the collapse of the northern cod stock in the early 1990's (Harris 1990; Bishop et al. 1993). We relate distributions in the 1990's to a historical distribution sampled in the 1980's, to current information on the spawning areas of northern cod, and to the predicted dispersal patterns of eggs and larvae. We observed differences in the geographic distributions of pelagic juvenile cod that correspond to differences in spawning by adults. Our second purpose was to measure the relative year-class strength of pelagic juvenile cod, as a prerecruit estimate. Finally, based on microotolith structure, we evaluate the spawning periods of the fall survivors, in relation to historic spawning patterns. Interannual differences in spawning period and abundance of juvenile cod are discussed in relation to spawning behaviour of adults and recruitment.

Methods

The sampling program consisted of a series of surveys that sampled inshore and offshore areas. During the first three years of the program, 1991–1993, sampling was carried out using one ship targeting the inshore areas along the northeast coast of Newfoundland and the offshore area of the southern Northeast Newfoundland Shelf and northern part of the Grand Bank (Fig. 1). The inshore area is defined by the large bays along the northeast coast of Newfoundland, including White Bay, Notre Dame Bay, Bonavista Bay, Trinity Bay, and Conception Bay (Fig. 1). Previous studies had indicated that these areas should cover the primary geographic distribution of pelagic juvenile cod (Helbig et al. 1992; Anderson et al. 1995; Davidson and deYoung 1995). Surveys were carried out from late August to the middle of October (Table 1) to precede the main period of settlement of the pelagic juvenile stage of cod. Settlement is thought to occur at approximately 60–80 mm length (Perry and Neilson 1988; Godo et al. 1989) and primarily from late October through November (Anderson and Dalley 1993; Methven and Bajdik 1994), although cod may settle earlier at smaller lengths in coastal habitats (Olsen and Soldal 1989; Methven and Bajdik 1994). In 1994 the survey was expanded to cover the entire area from Labrador to the southern tip of the Grand Bank using two ships simultaneously (NAFO Divisions 2J3KLNO, Fig. 1). The change to a broader survey area was intended to cover the entire geographic range of pelagic cod, which was not being sampled by the single-ship surveys. The shift to an earlier time in 1994 was to minimize any bias due to possible early settlement in some years. However, there was no indication that substantial settlement of juvenile cod had occurred prior to the start of the 1991–1993 surveys (Anderson and Dalley 1993).

Fig. 1. Geographical areas of the southern Labrador Shelf, Northeast Newfoundland Shelf, Grand Banks, and inshore bays located along the northeast coast of Newfoundland sampled in this study. Inshore area: WB, White Bay; NDB, Notre Dame Bay; BB, Bonavista Bay; TB, Trinity Bay; CB, Conception Bay. The open circles represent survey station locations. The isobath lines span depths from 100 to 1000 m.



A survey grid at 54-km (30 nautical mile) station spacing was used. This design is equivalent to a systematic stratified sampling design, where the first station is selected randomly from one 54 × 54 km stratum (Snedcor and Cochrane 1967). Within the inshore bays, stations were positioned approximately 54 km apart through the centre of each bay, as much as possible.

In 1991 the survey was carried out using a Tucker trawl. In 1992, both Tucker and International Young Gadoids Pelagic Trawl (IYGPT) trawls were used but both trawls were not used at all stations. In 1993 and 1994, only the IYGPT was used. The Tucker trawl had an effective opening of 4.5 m^2 and a mesh size of 3.2 mm in the main portion of the net and codend of 0.505-mm Nitex netting (Harding et al. 1987). It was towed at 1.25–1.5 $m \cdot s^{-1}$ using a double oblique haul 0-100 m with payout and retrieval rates of approximately 0.5 $m \cdot s^{-1}$. The Tucker trawl was instrumented and transmitted data in real time, including electronic flowmeters, net angle, and salinity–temperature–depth. The IYGPT is a pelagic midwater trawl designed to catch pelagic juvenile gadoids with an effective opening of approximately 10 × 10 m (Koeller and Carrothers 1981; Koeller et al. 1986; McCullum and Walsh 1995). In the 1992–1993 surveys the IYGPT was towed at 1.25–1.5 $m \cdot s^{-1}$ for 30 min with the head rope positioned at approximately 50–60 m depth. In 1994

© 1997 NRC Canada

Table 1. Summary of pelagic juvenile cod survey dates and sampling each year during 1991–1994.

Year	Start date	End date	Total days	Survey middate[a]	Number of stations	
					Tucker	IYGPT
1991	11 October	22 October	13	289	57	
1992	30 September	15 October	16	281	35	32
1993	27 September	20 October	24	281		87
1994	22 August	3 September	13	239		99

[a]Day of year.

the IYGPT was towed between 20 and 50 m depth. Depth and net configuration were monitored using acoustic net sensors (Scanmar) to measure net depth, net opening, and wing and door widths. For both trawls, the net performance data were used to estimate the volume of water (cubic metres) filtered during the tow.

Due to sampling problems the IYGPT and Tucker trawl were not used at all stations in 1992. A comparison of the standardized catch rates for 11 stations sampled by both trawls demonstrated that the Tucker trawl caught 4.3 cod·$(10^4\ m^3)^{-1}$ compared with 1.2·$(10^4\ m^3)^{-1}$ by the IYGPT (Anderson and Dalley 1993). Therefore, the standardized catch rates of the Tucker trawl were multiplied by a factor of 0.27 for direct comparison with IYGPT data.

The trawl catches were processed at sea identifying all fish to species level, where possible, and recording total length for Atlantic cod. Atlantic cod were preserved in 95% ethanol and returned to the laboratory where the otoliths (sagittae and lapillae) were removed and mounted on microscope slides using "crystal bond". Otoliths were polished to their central plane using different grades of lapping film. In most cases, lapillae were aged under a light microscope at magnifications of 400–1000 times with the assistance of an Optimus image analysis system. Replicate readings of daily rings were made to ensure consistency of the age estimates. When age estimates of replicate readings differed by more than 10%, the otolith was discarded. Independent estimates of otoliths were done for comparison of estimated ages. Samples for otolith age analyses were stratified across all length groups and for different geographic areas.

Comparison between means was based on the *t*-test, where the approximate *t*-statistic for unequal variances was used if the folded *F* statistic demonstrated that the variances between data sets were unequal (SAS Institute Inc. 1989). Distributions were contoured based on spatial interpolation of abundances ($\log_{10}$ number·$(10^4\ m^3)^{-1}$) using the kriging technique (Keckler 1994).

Results

Distributions and abundances

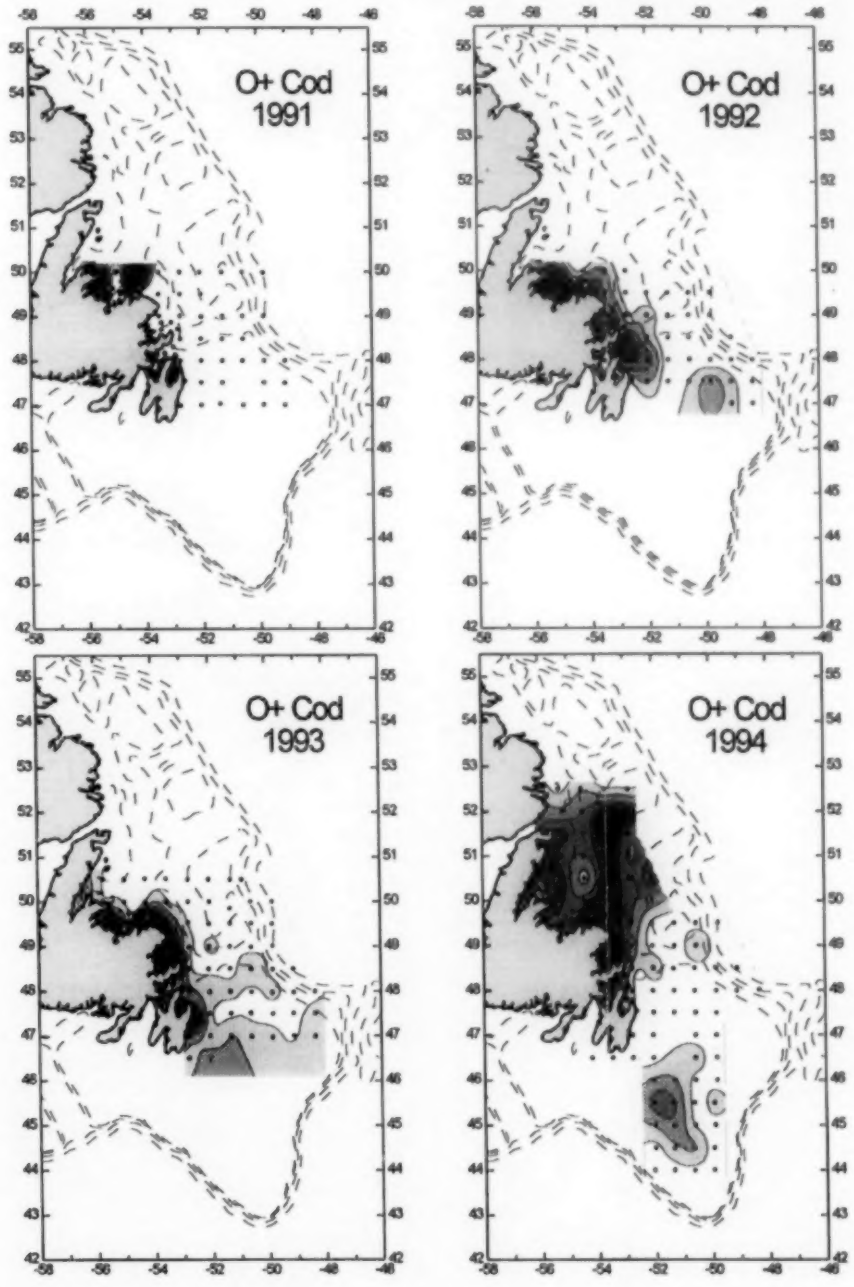
The pattern of distributions observed during the four years, 1991–1994, indicated a trend of expanding spatial distribution, both within the inshore areas and extending to the shelf areas offshore (Fig. 2). In 1991, pelagic juvenile cod were caught only at a few locations inshore and none were observed offshore. In 1992, cod were distributed throughout most of the inshore areas and on adjacent shelf areas, while a few cod were observed on the northern Grand Bank. By 1993, cod were again distributed widely within the inshore areas and on the adjacent shelf. However, they were also distributed more widely on the northern Grand Bank than in 1992. No cod were caught on the the southern portion of the Northeast Newfoundland Shelf sampled in the vicinity of Funk Island Bank during the first three years of this study. In 1994, cod were distributed throughout the inshore areas but were also observed over most of the sampled area of the Northeast Newfoundland Shelf, extending as far north as southern Labrador and over the sampled portions of Belle Isle Bank and Funk Island Bank. The greater offshore distribution on the Northeast Newfoundland Shelf in 1994 was evident when comparing 1994 stations in this area with corresponding ones from 1993. Few cod were caught on the northern Grand Bank in 1994, although a distinct concentration was sampled on the southern Grand Bank.

Comparison of abundances among years is confounded by the different gears used and the different extent of offshore sampling each year. In 1991, only the Tucker trawl was used and the number of cod captured was very low; only 15 cod were captured at 13 of 55 locations sampled. In 1992, both the IYGPT and Tucker trawl were used, but both trawls were not used at all locations. The very low abundance of cod sampled in 1991 is reinforced when comparing catches in the Tucker trawl at the same locations in 1992 where, on average, five times more cod were caught. Abundances (excluding zero catches) in the IYGPT averaged 1.9 cod·$(10^4\ m^3)^{-1}$ (range 0.4–8.8) in 1992, 0.8 cod·$(10^4\ m^3)^{-1}$ (range 0.5–3.8) in 1993, and 6.3 cod·$(10^4\ m^3)^{-1}$ (range 0.5–85.7) in 1994.

It is possible to compare mean abundances from the IYGPT within inshore and offshore areas from sample locations common among years (including zero catches). Mean abundance was highest in 1994, both inshore and offshore, and lowest in 1993 (Table 2). The maximum abundance sampled inshore in 1994 was almost an order of magnitude greater than in either 1992 or 1993, and offshore it was approximately three times greater. Comparison of abundances for commonly sampled inshore areas sampled by the IYGPT demonstrated that cod were significantly more abundant in 1994 and were lowest in abundance in 1993 (Table 3). Offshore cod were more abundant in 1994, while there was no statistical difference in abundance between 1992 and 1993 (Table 3). These statistical differences, combined with the apparent broad offshore distribution of cod in 1994, indicated that 1994 was a relatively large year-class compared with the previous three years. In contrast, year-class strength in 1991 appeared to be extremely low. While mean abundances were higher inshore in 1992 than in 1993, the broader distribution of cod offshore over the northern Grand Bank in 1993 may indicate a greater total number of cod offshore than in 1992.

© 1997 NRC Canada

Fig. 2. Abundance distributions of pelagic juvenile cod sampled during 1991–1994. Each year the distributions are contoured based on the abundance ($\log_{10}$number·$(10^4\ m^3)^{-1}$), scaled from highest to lowest within each year. The darkest shading represent areas of highest abundances. Contour levels are scaled within each year. Broken lines represent depth contours.



Lengths

Cod ranged in length from 26 to 88 mm across all years, with the predominant size ranging from 40 to 50 mm in 1992–1994 (Fig. 3). In 1991, cod ranged from 38 to 81 mm in length, although there were too few cod caught to determine length frequency modes. In 1992, cod ranged in length from 32 to 72 mm with a single mode centred at 46 mm. In 1993, there was a broader range of lengths sampled, from 26 to 88 mm with a dominant mode centred at 45 mm and a lesser mode centred at 65–66 mm. In 1994, there was again a single

© 1997 NRC Canada

Table 2. Mean and maximum abundances (number·(10^4 m^3)$^{-1}$) of pelagic juvenile cod caught by the IYGPT within common inshore and offshore locations sampled each year.

	Inshore[a]			Offshore		
Year	*n*	Mean	Maximum	*n*	Mean	Maximum
1992	18	1.066	1.160	15	1.025	1.116
1993	26	1.047	1.126	50	1.017	1.109
1994	23	1.506	9.569	76	1.138	3.378

Note: Means include null cathces; *n* = number of stations sampled.
[a]See Fig. 1 for inshore area.

Table 3. Statistical comparisons between mean abundances ($\log_{10}$ number·(10^4 m^3)$^{-1}$) from the IYGPT sampled within inshore and offshore locations each year.

	Inshore			Offshore		
Comparison	df	*t*	*P*	df	*t*	*P*
1992–1993	42	1.8024	0.0787	63	0.9653	0.3381
1992–1994	22.3	−3.3271	0.0030	85	−3.3282	0.0013
1993–1994	22.1	−3.5095	0.0020	77.3	−3.7055	0.0004

Note: *t* = *t*-test statistic; df = degrees of feedom where the fractions are the calculated degrees of freedom based on a test with unequal variances; *P* = probability that the means are statistically equivalent.

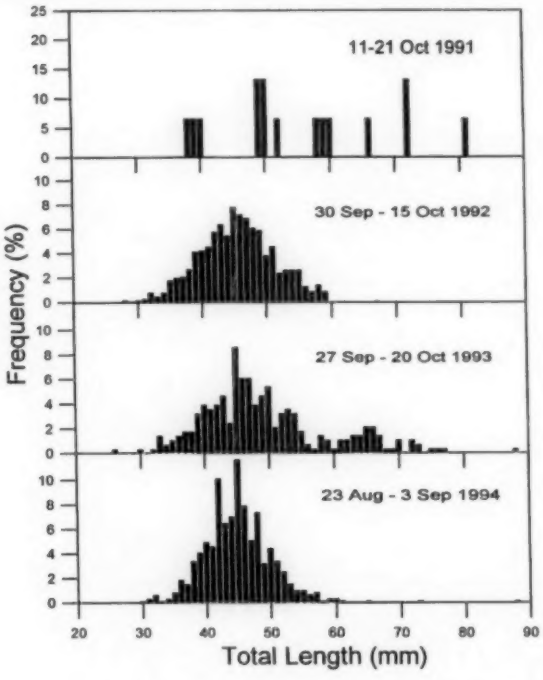
mode with a peak at 45 mm and lengths ranging from 30 to 73 mm.

Given the broader geographic area sampled in 1994, we examined lengths among the different areas in which cod were found. Cod ranged primarily between 31 and 64 mm in length in all areas with no apparent differences among areas. Inshore, cod averaged 43.4–46.7 mm (range 31–60) in length among all bays except Conception Bay. In Conception Bay, only five cod were caught, 40–101 mm in length. Cod off southern Labrador averaged 43.2 mm (range 33–56) in length and on the Northeast Newfoundland Shelf averaged 43.2 mm (range 32–58 mm) in length, while on the southern Grand Bank, cod averaged 49.6 mm (range 35–88) length. While the mean value on the southern Grand Bank was slightly greater, it was inflated by two fish of 73 and 87 mm length. The majority of fish measured on the southern Grand Bank ranged between 35 and 64 mm in length and averaged 47.3 mm.

Age and hatch dates

Cod ranged in age from 48 to 87 d (mean 67) in 1992, from 54 to 101 d (mean 69) in 1993, and from 58 to 121 d (mean 80) in 1994. The small number of fish captured and the poor quality of otoliths in 1991 precluded any ageing from these samples. Based on ages and the known date of capture, the hatch date of fall survivors in 1992 ranged from the middle of July to the middle of August with a peak in early August (Fig. 4). In 1993, hatching occurred from the end of June to the latter half of August. There were two distinct hatching periods in 1993. The first period occurred during the middle of July and the second during early August.

Fig. 3. Length frequency distributions sampled each year.



In 1994, hatching occurred significantly earlier than in 1992 and 1993, extending from the middle of May to the beginning of July and peaked throughout June.

Adjusted lengths

Growth rate averaged 0.65 mm · d^{-1} in 1992, 0.65 mm · d^{-1} in 1993, and 0.48 mm · d^{-1} in 1994 (Table 4). An analysis of covariance demonstrated that there was no statistical difference in growth rate between 1992 and 1993 but that growth rate was significantly slower in 1994 (Table 5). There was no statistical difference in intercepts between 1992 and 1993 (Table 5).

Based on the measured growth rates, the length frequencies of data collected during 1992–1994 were adjusted to match the middate (14 September) of a survey carried out in 1981 (Anderson et al. 1995). This adjustment permitted a direct comparison of cod lengths from the 1990's with the only historical data available from the offshore region. Compared with the length frequency distribution obtained in 1981, cod collected during 1992–1994 fell within the same range, primarily from 15 to 70 mm, but had different modes (Fig. 5). Lengths sampled in 1992 matched the length frequencies associated with the smallest fish sampled in 1981, which were those fish spawned latest in the season. In 1993, cod lengths were similar to the historic distribution sampled in 1981, although the dominant peak in 1993 was for late spawners. In comparison, it appears that the early spawners (largest lengths) were relatively less abundant. In 1994, there was a distinct shift in spawning from the late to the early period. Cod in 1994 fell within the range of the largest fish sampled in 1981, predominantly 50–60 mm based on adjusted lengths.

© 1997 NRC Canada

Table 4. Average growth rate estimated each year based on linear regressions of age (d) on total fish length (mm).

Year	Regression	df	F value	R^2 (%)
1992	Length = −0.46 + 0.648 age	102	111.18	51.9
1993	Length = −0.11 + 0.645 age	90	245.65	73.1
1994	Length = +6.86 + 0.476 age	100	81.24	45.1

Table 5. Statistical comparison (ANCOVA) of growth rates among years for all data where age was ≤80 d.

Years	df	Test F value	Slopes P level	Test F value	Intercepts P level
1992–1993	164	1.26	0.2629	0.05	0.8161
1992–1994	129	3.06	0.0824	NA	NA
1993–1994	94	0.86	0.3570	13.34	0.0004

Note: P level refers to the probability of obtaining a greater F value; NA, test not applicable.

Fig. 4. Larval hatch dates estimated from fish age at the time sampled each year, summarized into 5-d periods.

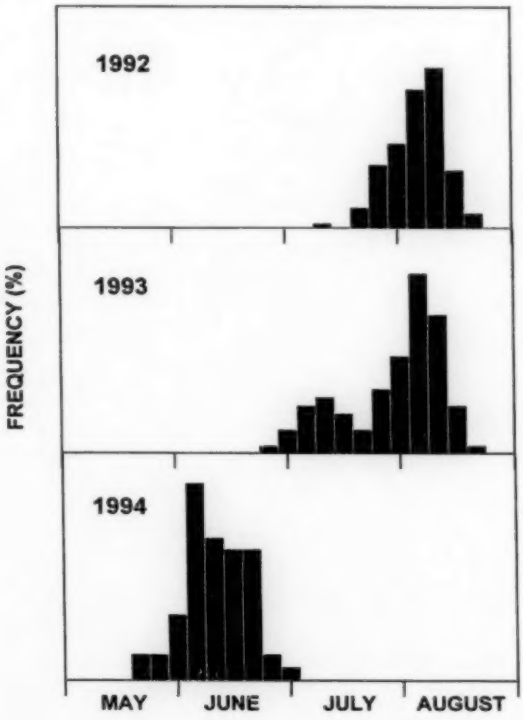
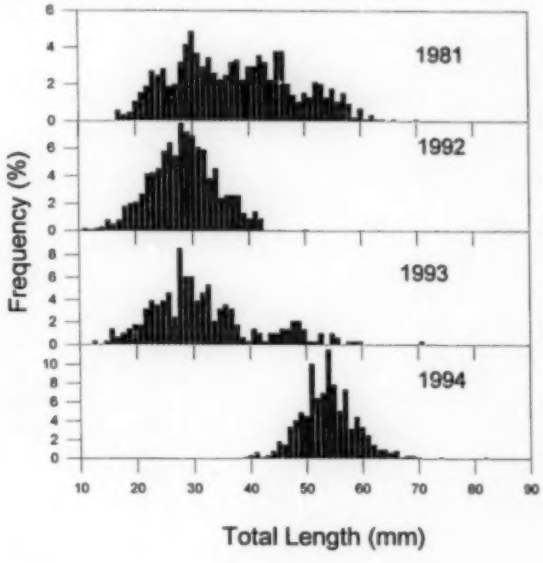


Fig. 5. Length frequency distributions adjusted to a common date in September based on measured growth rates in during 1992–1994 compared with the historic length frequency distribution sampled during September 1981.



Discussion

Year-class strength

Year-class strength is routinely estimated during the pelagic juvenile stage for a number of cod stocks in the North Atlantic. These estimates predict recruitment measured at older ages in most, but not all, years (Sundby et al. 1989; Asthorsson et al. 1994; Jakupsstovu and Reinert 1994). In some cases, high year-class strength measured during the pelagic juvenile stage does not result in high recruitment, apparently due to density-dependent predation occurring after settlement (Bogstad et al. 1994). For the northern cod stock (NAFO 2J3KL), we expect that abundance measured during the pelagic juvenile stage will also measure year-class strength in most years. Further, we suggest that there are three important measurements required to index year-class strength during the pelagic juvenile stage: abundance, size, and dis-

© 1997 NRC Canada

tribution. High abundance will indicate relatively high survival from spawning and may be linked to spawning stock biomass (Myers et al. 1993*a*; Bogstad et al. 1994). Relatively large sizes following the pelagic period may result in higher survival during the first year of life, both in relation to size-dependent predation (Ware 1975) and better condition for survival during the first winter (e.g., MacLean et al. 1981). Finally, spawning distributions relative to dispersal of cod eggs and larvae have been hypothesized as important to survival and recruitment in the northern cod (deYoung and Rose 1993). Specifically, spawning off southern Labrador is thought to favour high recruitment in northern cod, while spawning to the south is thought to be detrimental to recruitment.

Results from this study indicate a trend of increasing year-class strength during 1991–1994. The extremely low abundances and limited distribution of cod in 1991 indicated that year-class abundance was weak. In contrast, year-class strength in 1994 was significantly stronger than in the preceding three years, based on abundance, distribution, and size. Abundance in 1994 was significantly greater both inshore and offshore compared with the previous years. In addition, cod were distributed widely over the northern part of the Northeast Newfoundland Shelf, demonstrating that significant spawning occurred off southern Labrador in 1994. Finally, cod were larger in 1994 when compared at a common date than in 1992 or 1993. Although growth rate was lower in 1994, juveniles would still have been larger at the time of settlement in late November. Together, the greater abundance, larger size, and offshore distribution over the shelf in 1994 predict that eventual recruitment (at age 3) will be greater than in the previous three years.

The 1992 and 1993 year-classes may not have been significantly different in total abundance. Although mean abundance was greater inshore in 1992 than in 1993, there was no statistical difference offshore whereas the broader distribution in 1993 would have integrated into a greater total abundance. In addition, the presence of larger, older cod in 1993 would equate to more fish than in 1992 as a result of a greater cumulative mortality since hatching. Based on these considerations, we nominally rank year-class strength as 1994 $>$ 1993 $\geq$ 1992 $>$ 1991. The high ranking of the 1994 year-class and the low ranking of the 1991 year-class agree with estimates from bottom trawl surveys for these years (Dalley and Anderson 1997) and from an index of year-class strength based on beach seine surveys (Ings et al. 1997).

Direct comparisons of abundances sampled in 1994 with those measured in 1981 (Anderson et al. 1995) are confounded by differences in sampling gear and methods. However, several factors indicate that the abundance of pelagic juvenile cod in 1981 was much larger. Cod were distributed throughout the southern part of the Northeast Newfoundland Shelf and northern Grand Bank in 1981 (Anderson et al. 1995) whereas cod were not observed abundantly over the same area in 1994. In addition, there was a much broader range of lengths sampled in 1981, indicating a longer spawning period which would originate from a larger spawning stock with a greater age structure (Taggart et al. 1994). Finally, 1981 was one of the largest year-classes produced during the 1980's (Bishop et al. 1993).

Spawning areas

Historically, cod spawned throughout the inshore and offshore areas of the northern cod stock (2J3KL). However, the relative importance of spawning along the shelfbreak, versus over the shelf or within the inshore, is not known. The primary spawning areas were reported to be along the shelf break in association with the major offshore banks (Serebryakov 1967; Templeman 1981; Lear and Wells 1984). Hutchings et al. (1994) reported that spawning historically occurred more extensively over the shelf. However, Kulka et al. (1995) reported that the shelf break was a more important spawning area than the adjacent shelf during the 1980's and 1990's. The existence of local populations of cod within the inshore areas was recognized in early attempts to define management units for cod in the Newfoundland and Labrador region (Halliday and Pinhorn 1990) and has been confirmed by historical data (Hutchings et al. 1994). However, Anderson et al. (1995) estimated that the inshore areas may have represented no more than 10% of the population, compared with the offshore. Therefore, while spawning may occur almost anywhere, the shelf and outer shelf areas appear to have been the most important. deYoung and Rose (1993) hypothesized that spawning over the shelf in the north, and off southern Labrador, contributed most to the production of the northern cod stock.

Geographic distributions of pelagic juvenile cod largely result from drift during the egg and larval stages. Knowledge of ocean circulation can indicate probable spawning origins of these fish. Existing models of egg and larval drift predict that cod eggs spawned offshore will largely remain offshore, downstream of the spawning areas (Helbig et al. 1992; Davidson and deYoung 1995; Pepin and Helbig 1997). This prediction is supported by biological data which demonstrate that pelagic juvenile cod occurred abundantly over the Northeast Newfoundland Shelf and northern Grand Bank several months after spawning (Anderson et al. 1995). Some eggs and larvae spawned to the north and on the inner part of the shelf may drift inshore (Davidson and deYoung 1995; Pepin and Helbig 1996). However, these models predict that few cod eggs and larvae spawned at the shelf break will reach the inshore bays of eastern Newfoundland. The model predictions are supported by surface drogued drifters, few of which have entered the inshore bays from the offshore shelf (Myers et al. 1993*b*; Pepin and Helbig 1997).

A circulation model for Conception Bay predicts that eggs and larvae are dispersed from the bay (deYoung et al. 1994). For larvae originating near the innermost part of the bay, dispersal from the bay occurs on the order of 30 d, while dispersal times near the mouth of the bay are much less. Dispersal from the inshore bays is confirmed by observations of capelin larvae. During our surveys, larval capelin were found widely dispersed offshore, following a spawning that occurs on beaches entirely within the inshore area (Anderson and Dalley 1995).

In summary, existing models and data indicate that pelagic juvenile cod observed offshore will originate primarily from a spawning that occurred offshore, upstream on the shelf. Pelagic juvenile cod that occur inshore will originate primarily from a spawning that occurred inshore. In both cases, the circulation models predict that some mixing of eggs and

© 1997 NRC Canada

larvae between inshore and offshore spawning may occur as a result of drift.

The absence of pelagic juvenile cod in offshore samples during the first three years of this study, 1991–1993, indicates an absence of successful offshore spawning. However, in 1994, juvenile cod were observed abundantly over the Northeast Newfoundland Shelf, indicating that spawning had occurred off southern Labrador. In contrast, cod were observed throughout the inshore area during 1992–1994, consistent with successful inshore spawning.

These results are consistent with what is known about the remaining spawning concentrations of northern cod and predictions of egg and larval drift. During the 1980's, prespawning and spawning concentrations of cod were observed only in the north (Hamilton Bank and northern Belle Isle Bank) and middle (northern Funk Island Bank) part of their range, on the outer part of the shelf (Wroblewski et al. 1995). However, by 1990–1992, cod were observed only in the southern part of their range (south Funk Island Bank and northern Grand Bank) (Kulka et al. 1995). Similarly, spawning and postspawning concentrations of cod were observed to shift progressively to the south and east on the northern Grand Bank during the springs of 1990–1994 (deYoung and Rose 1993). The drift models predict that these southern spawning distributions would result in pelagic juvenile cod distributions over the Grand Bank, or that they would not be present at all due to advection off the shelf (Helbig et al. 1992; deYoung and Rose 1993; Davidson and deYoung 1995).

In June 1994, a postspawning concentration of cod was observed in the shelf area south of Hamilton Bank (G. Rose, Marine Institute, Memorial University of Newfoundland, St. John's, Nfld., personal communication). This observation is consistent with both the offshore distribution of pelagic juvenile cod observed in 1994 and the May spawning observed in this study.

Our results suggest that spawning occurred throughout the inshore areas during 1992–1994. The observed distributions are consistent with inshore spawning followed by dispersal of eggs and larvae to the offshore, as predicted by deYoung et al. (1994). Studies in Trinity Bay have confirmed the presence of spawning inshore during the 1990's (K. Smedbol, Memorial University of Newfoundland, St. John's, Nfld., personal communication). While some of the juvenile cod observed inshore may have originated from spawning offshore, this contribution is expected to be small based on (1) modelled predictions of dispersal, (2) the southern distribution of spawning cod offshore, which occurred primarily near the shelfbreak, and (3) the offshore distribution of pelagic juvenile cod observed in 1994, south of a spawning concentration observed near Hamilton Bank earlier in the year.

The discrete distribution of pelagic juvenile cod observed on the southern Grand Bank in 1994 is consistent with a distinct spawning on the southern Grand Bank, followed by retention of eggs and larvae over the Southeast Shoal. Previous work has demonstrated that eggs spawned on the southern Grand Bank are retained there through to larval and juvenile stages. Capelin, which spawn in shallow water on the Southeast Shoal, are retained there as larvae (Frank and Carscadden 1989). Similarly, larvae and juveniles of flatfish that have spawned on the southern Grand Bank are retained there as well (Walsh 1991; Frank et al. 1992).

Spawning periods

Historically, the spawning period of northern cod has extended from January to September with a tendency for cod to spawn earlier in the north, April, while in the south, spawning occurred in June (Myers et al. 1993*b*). Anderson et al. (1995) estimated that spawning peaked in April–May on the Northeast Newfoundland Shelf, and in June within the inshore areas, in the 1980's. Results from this study demonstrate that successful spawning, based on fall survivors, was restricted to relatively short periods, although these periods varied in timing among years.

Pelagic juveniles represent the survivors of spring and summer spawning. When abundances, distributions, sizes, and ages vary among years, it is difficult to distinguish between interannual differences in the spawning behaviour of adults versus differential survival during the egg and larval period, based on a single annual survey. However, there is evidence of a significant shift in spawning period to an earlier time in 1994.

In 1992, there was a single successful spawning period that occurred relatively late in the spawning season. Assuming egg development times of 25–30 d (Anderson and deYoung 1995), we estimate that spawning occurred primarily during July in 1992, based on peak hatching in August. In 1993, successful spawning occurred over a longer period of time, beginning in early June and extending through July, although the predominant period appeared to occur in July. In 1994, there was a single period of successful spawning, although this was much earlier than in 1992 or 1993, beginning in late April and occurring primarily through May. In 1994, there was no evidence of late spawning (June–July) as occurred in 1992 and 1993, based on bongo samples (61 cm, 0.333-mm mesh) collected during the pelagic juvenile survey (J. Anderson, unpublished data).

The results from 1994 suggest that the observed differences among years in spawning period were a function of changing spawning behaviour by the adults, versus differential survival of eggs and larvae from a protracted spawning period. Spawning that occurred in June and July of 1992 and 1993 was absent in 1994. Thus, spawning appeared to shift from July in 1992 to June–July in 1993 and then to April–May in 1994, a change on the order of 50–60 d. This observation contrasts with a stable spawning period that only varied by 5–7 d, and hatching that only varied by 2 wk over many years for the Arcto-Norwegian cod stock (Pedersen 1984; Ellertsen et al. 1989). However, our observation is supported by significant variations in cod spawning on the northern (3L) and southern (3NO) Grand Bank and on St. Pierre Bank (3Ps) (Hutchings and Myers 1994). On the northern Grand Bank the variance in spawning was 36 d, as 1 standard deviation about the mean, while the range in spawning was on the order of 50 d during the period 1948–1990.

The period of successful spawning was approximately two months in 1993 and only 1 mo in 1992 and 1994. Historically, spawning for the northern cod stock extended over several months (Myers et al. 1993*b*). Anderson et al. (1995) estimated that successful spawning occurred from early March to mid-June in 1981. It is reasonable to expect a contracted spawning period from the collapsed and reduced age structure of this stock (Hutchings and Myers 1993; Taggart et al. 1994). A shift in spawning period may be an adaptive strategy when spawning conditions change among years, par-

© 1997 NRC Canada

ticularly for a small population of cod with a reduced age structure.

Acknowledgements

We thank D. Riche, E. McDonald, T. Foulkes, D. Davis, and C. March for their expertise and assistance in carrying out the field sampling programs and for much of the data processing and analyses. Microotolith analyses were carried out by C. Mercer. Species verifications and some plankton processing were carried out by L. van Guelpen and staff at the Atlantic Reference Centre, St. Andrews, N.B. D. Riche, C. March, D. Orr, and T. Bolands were also responsible for plankton processing and species identifications. This work was supported as part of DFO's Northern Cod Science Program and also in 1994 by DFO's Interim Funding Research Program.

References

Anderson, J.T., and Dalley, E.L. 1993. Inshore/offshore distributions and abundances of pelagic 0-group cod in NAFO Divisions 3K and 3L in fall of 1991 and 1992. NAFO SCR Doc. 93/32, Ser. No. N2212.

Anderson, J.T., and Dalley, E.L. 1995. Distributions and abundances of pre-recruit capelin (*Mallotus villosus*) in the Newfoundland region, 1991–1994. DFO Atl. Fish. Res. Doc. 95/70. pp. 146–166.

Anderson, J.T., and deYoung, B. 1995. Development of a one-dimensional model of cod egg and larval vertical distributions on the Northeast Newfoundland Shelf. Can. J. Fish. Aquat. Sci. **52**: 1978–1989.

Anderson, J.T., Dalley, E.L., and Carscadden, J.E. 1995. Abundance and distribution of pelagic 0-group cod (*Gadus morhua*) in Newfoundland waters: inshore versus offshore. Can. J. Fish. Aquat. Sci. **52**: 115–125.

Assthorsson, O.S., Gislason, A., and Gudmundsdottir, A. 1994. Distribution, abundance, and length of pelagic juvenile cod in Icelandic waters in relation to environmental conditions. ICES Mar. Sci. Symp. **198**: 529–541.

Bishop, C.A., Murphy, E.F., Davis, M.B., Baird, J.W., and Rose, G.A. 1993. An assessment of the cod stock in NAFO Divisions 2J+3KL. NAFO SCR Doc. 93/86, Ser. No. N22271.

Bogstad, B., Lilly, G.R., Mehl, S., Palsson, O.K., and Stefansson, G. 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland and eastern Newfoundland). ICES Mar. Sci. Symp. **198**: 576–599.

Campana, S.E, Frank, K.T., Hurley, P.C.F., Koeller, P.A., Page, F.H., and Smith, P.C. 1989. Survival and abundance of young Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as indicators of year-class strength. Can. J. Fish. Aquat. Sci. **46**(Suppl. 1): 171–182.

Dalley, E.L., and Anderson, J.T. 1997. Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Davidson, F.J.M., and deYoung, B. 1995. Modeling advection of cod eggs and larvae on the Newfoundland Shelf. Fish. Oceanogr. **4**: 33–51.

deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. **50**: 2729–2741.

deYoung, B., Anderson, J., Greatbatch, R., and Fardy, P. 1994. Advection–diffusion modelling of larval capelin (*Mallotus villosus*) dispersion in Conception Bay, Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 1297–1307.

Ellertsen, B., Fossum, P., Solemdal, P., and Sundby, S. 1989. Relation between temperature and survival of eggs and first-feeding larvae of northeast Arctic cod (*Gadus morhua* L.). Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **191**: 209–219.

Frank, K.T. 1992. Demographic consequences of age-specific dispersal in marine fish populations. Can. J. Fish. Aquat. Sci. **49**: 2222–2231.

Frank, K.T., and Carscadden, J.E. 1989. Factors affecting recruitment variability of capelin (*Mallotus villosus*) in the Northwest Atlantic. J. Cons. Int. Explor. Mer, **45**: 146–164.

Frank, K.T., Loder, J.W., Carscadden, J.E., Leggett, W.C., and Taggart, C.T. 1992. Larval flatfish distributions and drift on the southern Grand Banks. Can. J. Fish. Aquat. Sci. **49**: 467–483.

Godo, O.R., Gjosaeter, J., Sunnana, K., and Dragesund, O. 1989. Spatial distribution of 0-group gadoids off mid-Norway. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **191**: 273–280.

Halliday, R.G., and Pinhorn, A.T. 1990. The delimitation of fishing areas in the Northwest Atlantic. J. Northwest. Atl. Fish. Sci. **10**: 1–51.

Harding, G.C., Pringle, J.D., Vass, W.P., Pearre, Jr., S., and Smith, S.J. 1987. Vertical distribution and daily movements of larval lobsters *Homarus americanus* over Brown's Bank, Nova Scotia. Mar. Ecol. Prog. Ser. **41**: 29–41.

Harris, L. 1990. Independent review of the state of the northern cod stock. Department of Fisheries and Oceans, Communications Directorate, Ottawa, Ont.

Helbig, J., Mertz, G., and Pepin, P. 1992. Environmental influences on the recruitment of Newfoundland/Labrador cod. Fish. Oceanogr. **1**: 39–56.

Hutchings, J.A., and Myers, R.A. 1993. The effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2468–2474.

Hutchings, J.A., and Myers, R.A. 1994. Timing of cod reproduction: interannual variability and the influence of temperature. Mar. Ecol. Prog. Ser. **108**: 21–31.

Hutchings, J.A., Myers, R.A., and Lilly, G.R. 1994. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2457–2467.

Ings, D.W., Schneider, D.C., and Methven, D.A. 1997. Detection of a recruitment signal in juvenile Atlantic cod (*Gadus morhua*) in coastal nursery areas. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Jakupsstovu, S.H., and Reinert, J. 1994. Fluctuations in the Faroe Plateau cod stock. ICES Mar. Sci. Symp. **198**: 194–211.

Keckler, D. 1994. SURFER for Windows, contouring and 3D surface mapping. User's guide. Golden Software Inc., 809 14th Street, Golden, CO 80401-1866, U.S.A.

Koeller, P., and Carrothers, P.J.G. 1981. Cruise report, R/V *Lady Hammond* H051. Purpose: to determine the optimum rigging for the International Young Gadoid Pelagic Trawl (IYGPT) on the R/V *Lady Hammond*. Department of Fisheries and Oceans, Marine Fish Division, Bedford Institute of Oceanography, Dartmouth, N.S.

Koeller, P.A., Hurley, P.C.F., Perley, P., and Neilson, J.D. 1986. Juvenile fish surveys on the Scotian Shelf: implications for year-class size assessments. J. Cons. Int. Explor. Mer, **43**: 59–76.

Kulka, D.W., Wroblewski, J.S., and Narayanan, S. 1995. Recent changes in the winter distribution and movements of northern Atlantic cod (*Gadus morhua* Linnaeus, 1758) on the Newfoundland–Labrador shelf. ICES J. Mar. Sci. **52**: 889–902.

Lear, W., and Wells, R. 1984. Vertebral averages of juvenile cod, *Gadus morhua*, from coastal waters of eastern Newfoundland and Labrador as indicators of stock origin. J. Northwest Atl. Fish. Sci. **5**: 23–31.

MacLean, J.A., Shuter, B.J., Regier, H.A., and MacLeod, J.C. 1981. Temperature and year-class strength of smallmouth bass. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **178**: 30–40.

© 1997 NRC Canada

McCullum, B.R., and Walsh, S.J. 1995. Survey trawl reference manual. Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Nfld.

Methven, D.A., and Bajdik, C. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 78–90.

Myers, R.A., Drinkwater, K.F., Barrowman, N.J., and Baird, J.W. 1993*a*. Salinity and recruitment of Atlantic cod (*Gadus morhua*) in the Newfoundland region. Can. J. Fish. Aquat. Sci. **50**: 1599–1609.

Myers, R.A., Mertz, G., and Bishop, C.A. 1993*b*. Cod spawning in relation to physical and biological cycles of the northern Northwest Atlantic. Fish. Oceanogr. **2**: 154–165.

Olsen, S., and Soldal, A.V. 1989. Observations on inshore distribution and behaviour of 0-group northeast Arctic cod. Rapp. P.-v. Réun. Cons. int. Explor. Mer, **191**: 296–302.

Pedersen, T. 1984. Variation of peak spawning of Arcto-Norwegian cod (*Gadus morhua* L.) during the time period 1929–1982 based on indices estimated from fishery statistics. *In* The propagation of cod *Gadus morhua* L. *Edited by* E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Flodevigen Rapp. 1. Flodevigen Biological Station, Arendal, Norway. pp. 301–316.

Pepin, P., and Helbig, J.A. 1997. Distribution and drift of cod eggs and larvae on the northeast Newfoundland Shelf. Can. J. Fish. Aquat. Sci. **54**. (In press)

Perry, R.I., and Neilson, J.D. 1988. Vertical distributions and trophic interactions of age-0 Atlantic cod and haddock in mixed and stratified waters of Georges Bank. Mar. Ecol. Prog. Ser. **49**: 199–214.

Polacheck, T., Mountain, D., McMillan, D., Smith, W., and Berrien, W. 1992. Recruitment of the 1987 year class of Georges Bank haddock (*Melanogrammus aeglefinus*): the influence of larval transport. Can. J. Fish. Aquat. Sci. **49**: 484–496.

Riley, J.D., and Parnell, W.G. 1984. The distribution of young cod. *In* The propagation of cod *Gadus morhua* L. *Edited by* E. Dahl, E.S. Danielssen, E. Moksness, and P. Solemdal. Flodevegen Rapp. 1. Flodevigen Biological Station, Arendal, Norway. pp. 563–580.

Rose, G.A., Atkinson, B.A., Baird, J., Bishop, C.A., and Kulka, D.W. 1994. Changes in distribution of Atlantic cod and thermal variations in Newfoundland waters, 1980–1992. ICES Mar. Sci. Symp. **198**: 542–552.

SAS Institute Inc. 1989. SAS/STAT user's guide, release 6.03 edition. SAS Institute Inc., Cary, N.C.

Schopka, S.A. 1994. Fluctuations in the cod stock off Iceland during the twentieth century in relation to changes in the fisheries and environment. ICES Mar. Sci. Symp. **198**: 175–193.

Serebryakov, V. 1967. Cod reproduction in northwest Atlantic. Tr. Polyarn. Nauchno-Issled. Proektn. Inst. Morsk. Rybn. Khoz. Okeanog. (PINRO), **20**: 205–242. (Fish. Res. Board Can. Transl. Ser. No. 1133)

Snedcor, G.W., and Cochrane, W.G. 1967. Statistical methods. The Iowa State University Press, Ames, Iowa.

Sundby, S., Bjorke, H., Soldal, A.V., and Olsen, S. 1989. Mortality rates during the early life stages and year-class strength of northeast Arctic cod (*Gadus morhua*). Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **191**: 351–358.

Suthers, I.M., and Frank, K.T. 1989. Inter-annual distributions of larval and pelagic juvenile cod (*Gadus morhua*) in southwestern Nova Scotia determined with two different gear types. Can. J. Fish. Aquat. Sci. **46**: 591–602.

Suthers, I.M., and Sundby, S. 1993. Dispersal and growth of pelagic juvenile Arcto-Norwegian cod (*Gadus morhua*), inferred from otolith microstructure and water temperature. ICES J. Mar. Sci. **50**: 261–270.

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

Templeman, W.T. 1981. Vertebral numbers in Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas, 1947–71, and their use for delineating stocks. J. Northwest Atl. Fish. Sci. **2**: 21–45.

Templeman, W.T. 1989. Variation of vertebral numbers with fish length in Atlantic cod (*Gadus morhua*) of the eastern Newfoundland area, 1947–71. J. Northwest Atl. Fish. Sci. **9**: 45–52.

Walsh, S.J. 1991. Commercial fishing practices on offshore juvenile flatfish nursery grounds on the Grand Banks of Newfoundland. Neth. J. Sea Res. **27**: 423–432.

Ware, D.M. 1975. Relation between egg size, growth and natural mortality of larval fish. J. Fish. Res. Board Can. **32**: 2503–2512.

Wroblewski, J.S., Kulka, D.W., Narayanan, S., Oake, A., Collier, A., and McGrath, B. 1995. Winter distribution and movements of northern Atlantic cod (*Gadus morhua*) along the Newfoundland–Labrador continental shelf edge derived from observations on commercial trawlers. Fish. Oceanogr. **4**: 128–146.

© 1997 NRC Canada

Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland

E.L. Dalley and J.T. Anderson

Abstract: Demersal juveniles of the 2J3KL northern cod (*Gadus morhua*) stock complex were widely distributed in inshore and offshore areas of NAFO Division 3KL during early winter (1992–1994), following stock collapse. Catch rate at ages 0 and 1 was inversely related to bottom depth in all three years. Catch rate at age 3 was positively related to depth in two of the three years and positively related to bottom temperature all three years. An ontogenetic pattern in distribution existed whereby age 0 fish were distributed almost exclusively in the inshore, age 1 fish extended further onto shelf areas, and larger juveniles were widely distributed on the shelf. With increasing age, there was a logarithmic decrease in the ratio of mean catch rate inshore compared with offshore. Significant differences in catch rates at ages 2 and 3 support the concept of a decrease in year-class strength each year from 1989 to 1991. Apparent increases in mean catch rate of age 0 and 1 fish in 1993 and 1994 were not statistically higher than that of 1992. The observations are discussed in relation to inshore and offshore spawning and future surveys designed to minimize bias in indices of prerecruit abundance, during the rebuilding phase of the northern cod stock complex.

Résumé : Suite à l'effondrement du complexe de stocks de morue du Nord (*Gadus morhua*) de 2J3KL, les juvéniles démersaux étaient largement répandus dans les zones côtières et hauturières de la division 3KL au cours des premiers mois d'hiver (1992 à 1994). Le taux de capture pour les poissons d'âge 0 et d'âge 1 était inversement proportionnel à la profondeur du fond au cours des trois années. Le taux de capture pour les poissons d'âge 3 était directement proportionnel à la profondeur pour deux des trois années; ce taux était directement proportionnel à la température de fond au cours des trois ans. La distribution des poissons se faisait suivant un modèle ontogénique : les poissons d'âge 0 se retrouvaient presque exclusivement dans la zone côtière, les poissons d'âge 1 occupaient davantage les zones du plateau, et les juvéniles plus gros étaient largement répandus sur le plateau. Nous avons noté qu'une augmentation de l'âge était liée à une diminution logarithmique du rapport entre le taux moyen de capture dans la zone côtière et dans la zone hauturière. Les différences significatives observées dans les taux de capture à l'âge 2 et à l'âge 3 confirment la notion que, chaque année de 1989 à 1991, il y a eu réduction de l'effectif des classes d'âge. Les augmentations observées dans les taux moyens de capture pour les poissons d'âge 0 et d'âge 1 en 1993 et 1994 par rapport aux taux de 1992 n'étaient pas statistiquement significatives. Nous situons ces observations par rapport à la fraye dans les zones côtières et hauturières, et nous abordons la conception d'études futures visant à minimiser les biais dans les indices d'abondance des prérecrues, au cours de la phase de reconstruction du complexe de stocks de la morue du Nord.
[Traduit par la Rédaction]

Introduction

Landings from the northern cod (*Gadus morhua*) stock complex (NAFO Divisions 2J3KL) had fallen to record low levels (Taggart et al. 1994) prior to the stock being closed to commercial fishing in 1992. Rebuilding of this stock complex to near historical levels will depend on significant recruitment over a number of years.

Recruitment of Atlantic cod is often established by the pelagic 0-group stage (Campana et al. 1989; Sundby et al. 1989; Assthorsson et al. 1994; Jakupsstovu and Reinert 1994) which occurs during a relatively short period (2–4 mo) following metamorphosis from the larval stage, prior to settling to a demersal habitat. Sissenwine (1984), however, hypothesized that events during the demersal prerecruit stage (which follows the pelagic stage) are important in determining recruitment. Mehl (1989) and Bogstad et al. (1994) have shown that density-dependent predation on demersal juveniles (ages 0–2 yr) can significantly reduce recruitment in some cases.

Estimates of abundance of prerecruit cod at successive ages would provide an early signal of population growth during the rebuilding phase. However, in the case of the northern cod stock complex, systematic measures of abundance of demersal prerecruits, throughout the vast geographic area potentially available to the stock, have not been implemented.

Demersal juvenile cod are known historically to occur in offshore Newfoundland waters. Age 0 demersal cod occurred in low numbers on the shelf, more frequently from north to south (2J to 3L) in the December–January period, 1962–1963 (Bulatova 1963). Bogstad et al. (1994) also showed that age 0 demersal cod occurred off Labrador and on the northeast Newfoundland shelves. In winter (December–March), juveniles (ages 0–3) extended throughout the shelf

Received March 27, 1995. Accepted June 6, 1996.
J13511

E.L. Dalley and J.T. Anderson. Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

© 1997 NRC Canada

areas of Labrador (Divisions 2GHJ), on the Northeast Newfoundland Shelf (Division 3K), and on the Grand Banks (Divisions 3LNO) (Bulatova 1971). Young cod (1–2 yr old) also occurred throughout Divisions 3KL in the spring (Bulatova 1970, 1980, 1990; Kuzmin and Tevs 1991). In the fall, age 3–4 cod were known to be more widely distributed than age 1 cod which occurred more frequently on the inner Northeast Newfoundland Shelf and on the edge of the northern Grand Bank (Anderson 1993). In all these cases, data from offshore areas were limited by sampling trawls that had low catchabilities for young cod, particularly those younger than 3 yr old (e.g., Bulatova 1962; Godo and Walsh 1992). Most importantly, these surveys did not sample the inner shelves or within any of the large northeast Newfoundland bays.

Juveniles have also been seasonally abundant in the shallow nearshore areas of the northeast coast of Newfoundland (Lear et al. 1980; Keats et al. 1987; Clark and Green 1990; Keats 1990; Methven and Bajdik 1994; Anderson and Dalley 1995; Schneider et al. 1997), and diel variability in distribution has been noted (Keats 1990; Keats and Steele 1992; Methven and Badjik 1994). These inshore studies used various sampling techniques that differed from those used in the offshore, such that historic catch comparisons between inshore and offshore data are not possible.

This paper describes the results of a 3-yr study to determine distribution of age 0–3 juvenile cod in inshore and offshore locations, following the collapse of the northern cod stock. Catch rate is examined in relation to water depth and bottom temperature and for annual and diel (considering nearshore observations) differences in catch rate. Baseline information is essential for designing surveys for prerecruit abundance and as reference levels during the rebuilding phase.

Methods and materials

Fixed sampling stations were located within each of the five major bays along the northeast coast of Newfoundland and along six transects that extended from 37–55 km off the coast across the shelf to the shelf break (Fig. 1). Surveys were carried out in December 1992, December 1993 – January 1994, and December 1994 – January 1995 and will be referred to as the 1992, 1993, and 1994 surveys, respectively (Table 1). Considerations of survey duration took precedence over smaller scale spatial variability in the survey design to cover a large geographic area in as short a time as possible. An effort was made to find trawlable sites within each 100-m depth contour, of each transect, and within each bay (minimum depth ~60 m). This was not always possible because rough bottom rendered some areas "untrawlable", particularly in the inshore. Distance between stations did not exceed 55 km.

The sampling trawl was a three-bridle Campelen 1800-mesh shrimp trawl with 60- to 80-mm stretched meshes at the front which decreased to 44 mm in the codend (Engas and Godo 1989). In 1993 and 1994, we added a 10.2-m-long, 12.7-mm-mesh codend liner. The trawl was outfitted with 14-in. (36-cm) rubber disc rockhopper groundgear and 1400-kg polyvalent doors. Trawl performance was monitored using SCANMAR (Koeller et al. 1994) sensors. Generally the vertical height was 3.5–4.5 m, wing spread was 15–18 m, and door spread was 20–40 m. Effort at each station was standardized by fishing on bottom for 30 min at a ship's speed of 6.5 km·h^{-1}. Temperature and bottom depth along the tow path were recorded every 10 s using a trawl-mounted CTD (conductivity–temperature–depth) unit. Juvenile cod were defined as those <391 mm total length, which was the length selected from available age–length keys at the time to ensure inclusion of age 3 fish. Juveniles were sorted from the catch prior to onboard biological sampling. We sampled sagittal otoliths in a random stratified manner to ensure ageing across all sizes. To accommodate the timing of the 1993 and 1994 survey, "birth dates" were defined as 1 February rather than 1 January. An age–length key was derived for each survey and applied to the length frequency distribution standardized by catch rate (Fig. 2) to obtain numbers at age for each station.

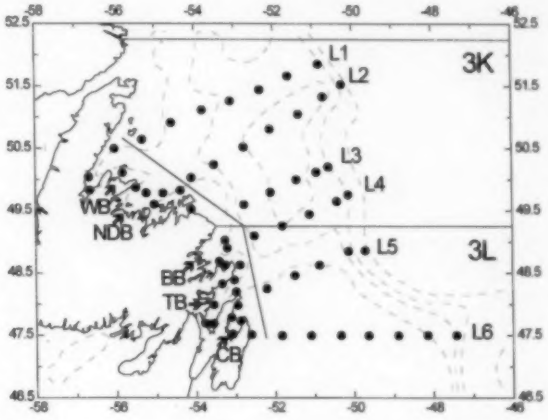


Fig. 1. Map of inshore/offshore northeast Newfoundland showing the positions of stations sampled during demersal juvenile cod surveys on the *Wilfred Templeman*, 1992–1994. The black line along the northeast coast delineates inshore from offshore stations. WB, NDB, BB, TB, and CB represent White, Notre Dame, Bonavista, Trinity, and Conception Bay, respectively; L1–L6 represent transect lines 1–6.

Pearson's correlation analysis was carried out on $\log_{10}$ (catch rate + 1) and environmental variables (bottom depth and temperature). A standard two-way ANOVA, with interaction, was performed to investigate diel and year effects on $\log_{10}$ (catch rate + 1) at age. Year (1992, 1993, or 1994) and day/night (daylight or darkness) were used as independent variables. Differences in years were examined a posteriori using Duncan's multiple range test. Statistical analyses were carried out using SAS (SAS Institute Inc. 1989).

Results

Environmental factors

Mean catch rate, by age, varied from a low of 1 fish · tow^{-1} for age 3 cod to a high of 55 fish · tow^{-1} for age 1 cod, both recorded in 1994 (Table 2). Maximum total catch rate (all ages combined) was 2910 fish · tow^{-1} taken in Trinity Bay in 1994. Maximum catch rates each year were 344 age 2 cod in 1992, 634 age 1 cod in 1993, and 1996 age 1 cod in 1994. Depths and temperature ranges were similar each year. During all three years, there was a statistically significant ($p < 0.001$) inverse correlation between catch rate of age 0 and 1 juvenile cod and water depth (Table 3). In 1992 and 1993, there were weak correlations ($p < 0.05$), which were opposite in sign, between catch rate of age 2 cod and water depth. In 1993 and 1994, there was a significant positive correlation ($p < 0.0005$) between catch rate of age 3 cod and depth.

There was no statistical correlation between catch rate of age 0, 1, or 2 cod and temperature. However, for all three

© 1997 NRC Canada

Table 1. List of research vessel trips on the *Wilfred Templeman* comprising the 1992, 1993, and 1994 demersal juvenile cod surveys in inshore/offshore northeast Newfoundland.

Survey year	Trip No.	Trip dates	Number of successful sets
1992	131	2–15 Dec. 1992	64
1993	147	7–16 Dec. 1993	41
	148	4–13 Jan. 1994	22
1994	163	10–20 Dec. 1994	27
	164	4–13 Jan. 1995	39

Table 2. Summary statistics for depth, temperature, and catch rate (no. of juvenile cod·30-min tow^{-1}), by age, for demersal juvenile cod surveys carried out in inshore/offshore northeast Newfoundland, 1992–1994 (numbers in parentheses represent standard deviation of the means).

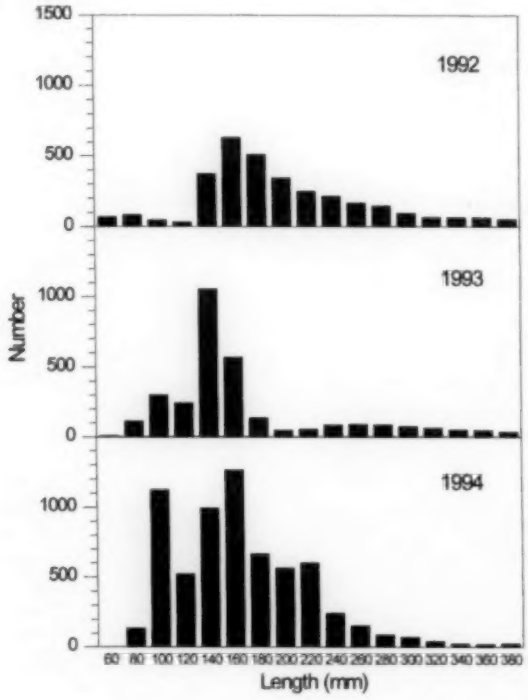
Age	Mean	Min.	Max.
1992 (N = 64)			
All ages	51.85 (113.4)	0	548
Age 0	3.21 (12.7)	0	74
Age 1	15.16 (43.1)	0	285
Age 2	27.03 (60.6)	0	344
Age 3	6.45 (9.5)	0	47
Depth	237.25 (119.3)	59	603
Temperature	0.46 (1.5)	−1.3	3.8
1993 (N = 63)			
All ages	52.22 (132.2)	0	820
Age 0	6.17 (24.3)	0	173
Age 1	36.41 (109.3)	0	634
Age 2	6.62 (10.4)	0	74
Age 3	3.02 (9.4)	0	73
Depth	237.00 (117.1)	59	615
Temperature	0.42 (1.7)	−1.5	3.9
1994 (N = 66)			
All ages	99.89 (386.9)	0	2910
Age 0	23.67 (109.5)	0	870
Age 1	55.42 (255.5)	0	1996
Age 2	19.74 (95.4)	0	776
Age 3	1.06 (2.9)	0	16
Depth	232.17 (109.1)	58	582
Temperature	0.53 (1.5)	−1.3	3.7

years, there was a significant positive relationship ($p < 0.01$) between catch rate at age 3 and temperature (Table 3).

Diel and annual effects

An ANOVA model for catch rate using year and day/night as independent variables indicated that the overall model explained a low (20%) but significant ($p < 0.0001$) portion of variability in catch rate for age 3 cod only (Table 4). The sums of squares partitioned to day/night did not contribute significantly at any age, any year. However, the year effect was significant at age 2 ($p < 0.05$) and age 3 ($p < 0.0001$). Duncan's multiple range test indicated that catch rate of the

Fig. 2. Juvenile cod length frequency distributions, by year (weighted by CPUE), for all sets combined from demersal trawl surveys carried out in inshore/offshore northeast Newfoundland, 1992–1994. Lengths indicated are approximate midpoints of 20-mm length-classes (e.g., 60 = 51–70 mm, 80 = 71–90 mm, etc.).



1990 year-class at age 2 was significantly higher than that of the 1991 or 1992 year-class, which was not significantly different at the same age. At age 3, the catch rate of the 1989 year-class was significantly higher than that of the 1990 year class which in turn was significantly higher than that of the 1991 year class. No significant differences were found in mean catch rate at age 0 or 1 for any of the three years.

Distributions

Juvenile cod were distributed throughout the survey area, inshore and offshore, during 1992–1994. Of tows throughout this period, only 17 recorded zero catches (five in each of 1992 and 1993 and seven in 1994). Catch rate at all ages was generally low in White and, particularly, Bonavista bays compared with the other inshore locations.

The distribution of age 0 cod was almost exclusively restricted to the inshore areas during all three surveys (Fig. 3). In all three years, only a single individual each year was found further than ~55 km from the coast. Age 0 cod were found in all five northeast coast bays (Conception Bay to White Bay), but not in all years. Although the highest single catch rate of age 0 cod (1996 fish) was taken in Trinity Bay in 1994, relatively high catch rates occurred in Conception and Trinity bays all three years and in Notre Dame Bay in 1993 and 1994.

Highest catch rates of age 1 cod also occurred in the

© 1997 NRC Canada

Table 3. Pearson's correlation coefficients (and associated probabilities) for relationships between $\log_{10}$ abundance of juvenile cod, by age, and temperature and depth during demersal surveys carried out in inshore/offshore northeast Newfoundland, 1992–1994.

	Age 0	Age 1	Age 2	Age 3
1992				
Depth	–0.444	–0.464	–0.276	0.041
	0.0002	0.0001	0.0273	0.7469
Temperature	0.059	–0.109	0.059	0.331
	0.6433	0.3928	0.6430	0.0075
1993				
Depth	–0.520	–0.543	0.290	0.514
	0.0001	0.0001	0.0212	0.0001
Temperature	–0.100	–0.232	0.218	0.414
	0.4342	0.0677	0.0857	0.0007
1994				
Depth	–0.544	–0.392	0.095	0.416
	0.0001	0.0011	0.4468	0.0005
Temperature	–0.205	–0.169	0.233	0.443
	0.0989	0.176	0.059	0.0002

inshore, particularly Trinity and Conception bays, in all three years (Fig. 4). The single highest catch rate was taken in Trinity Bay in 1994. Although there was a greater utilization of the shelf area by age 1 than by age 0 cod, only low numbers occurred near the shelf edge.

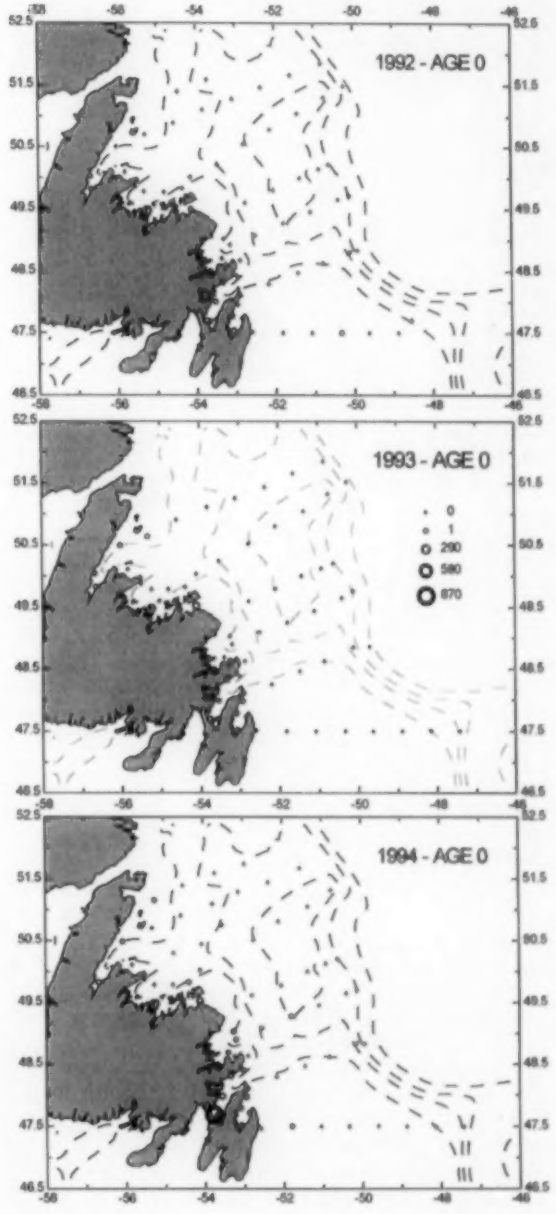
Two-year-old cod were distributed inshore and offshore (Fig. 5), but more widely in the offshore than age 1 cod. In 1992 and 1994, highest catch rates occurred in the two southern bays and the largest single catch was again in Trinity Bay in 1994. Very few age 2 cod were taken on the most southerly transect line across the Northern Grand Bank. Catch rates in 1993 (1991 year-class) were low throughout the survey area.

Distribution of age 3 cod was relatively widespread (Fig. 6). Mean catch rate was lowest for any age group in 1993 and 1994. Zero catches were frequent in the inshore, particularly in 1994 (1991 year-class). Catches were high in Trinity and Conception bays in 1992, but overall catch rates of age 3 cod were low inshore compared with those of other ages. Relatively high catch rates were taken near the shelf edge during all three years.

With increasing age, there was a consistent decrease in the catch rate of juvenile cod in the inshore compared with the offshore area (Fig. 7). At age 0 the catch rate inshore was several orders of magnitude greater than offshore. At age 1, it was one to two orders of magnitude higher inshore, while at age 2, it was up to 10 times higher inshore. By age 3, mean catch rate was higher in the offshore in two of the three years surveyed.

Due to between-year differences, no consistent trends in relative abundance were visible at any age in the northern (3K) portion relative to the southern (3L) portion of the survey area (Table 5). This was particularly true of the offshore where the only comparisons with historic distribution trends between areas could be made. The only consistency was in inshore areas where mean catch rate of age 1 cod was consistently higher in 3L in all three years.

Fig. 3. Distribution of age 0 juvenile cod sampled during demersal trawl surveys carried out in inshore/offshore northeast Newfoundland, 1992–1994. The expanding symbols represent a linear scale based on catches per 30-min tow. Crosses represent zero catches.



Discussion

During early winter 1992–1994, demersal juvenile cod utilized habitats within each of the large northeast coast bays, throughout the Northeast Newfoundland Shelf, and on the Northern Grand Banks (NAFO Division 3KL). There was a clear ontogenetic pattern in distribution. Age 0 juveniles

© 1997 NRC Canada

Table 4. Results of two-way ANOVA of $\log_{10}$ catch rates of juvenile cod, by age, using year and day/night as independent variables for demersal surveys carried out in inshore/offshore northeast Newfoundland, 1992–1994 (shown is the overall model fit and the contribution of each variable and interaction (year × day/night) when the total sums of squares are partitioned).

Overall model fit				Partial sums of squares			
Age	r_2	F	Pr > F	Source	Type III SS	F value	Pr > F
0	0.03	1.22	0.3024	Year	1.414	2.14	0.1206
				Day/night	0.070	0.21	0.6471
				Interaction	0.294	0.44	0.6418
1	0.02	0.76	0.5788	Year	1.114	1.02	0.3626
				Day/night	0.036	0.07	0.7977
				Interaction	0.423	0.39	0.6795
2	0.04	1.54	0.1781	Year	2.443	3.65	0.0278
				Day/night	0.011	0.03	0.8556
				Interaction	0.405	0.61	0.5465
3	0.20	9.55	0.0001	Year	7.356	23.63	0.0001
				Day/night	0.002	0.01	0.9111
				Interaction	0.387	1.24	0.2912

occurred almost exclusively within the large northeast coast bays. At age 1, catch rates were much higher inshore compared with offshore, but age 1 fish were dispersed onto shelf areas at depths up to 400 m. Mean catch rates of age 2 fish were also higher inshore for two of the three years. However, mean catch rate of age 3 cod was higher offshore for two of the three years. These age-dependent distributions are consistent with those observed for age 1–4 cod during random stratified groundfish surveys in the offshore area (Anderson 1993). The observations illustrate, for the years surveyed, that the relative utilization of inshore compared with offshore habitats is extensive and that age 0 settlement occurred almost exclusively in the inshore.

The significant correlations between catch rate of age 0 and 1 juveniles and depth resulted from the fact that stations fished in the inshore, where most younger juveniles were captured, were shallower than those on the shelf. Minimum depth fished here was ~60 m, significantly deeper than the nearshore where high numbers of age 0–1 cod occur seasonally (Lear et al. 1980; Keats et al. 1987; Clark and Green 1990; Keats 1990; Schneider et al. 1997; Ings et al. 1997). None of these inshore studies have extended beyond 10–20 m depth. Recently, however, Anderson and Dalley (1995) demonstrated that the abundance of age 0 and 1 cod extended away from shore at selected sites to approximately 40–60 m depth.

The positive relationship between catch rate of age 3 fish and temperature was not expected a priori. Goddard et al. (1992) found that juvenile northern cod (including age 3 cod) are capable of high freeze resistance in winter. Colder bottom temperatures prevail in the inshore (mean = −0.12 to −0.32°C) compared with the offshore (mean = 0.84–1.01°C). Age 3 cod were, however, associated with warmer water in all three years (and also greater depth in two of the three years) compared with age 0 and 1 cod. Age 2 cod appeared to be intermediate between younger juveniles that preferred shallower water and the larger age 3 cod that appeared to prefer the warmer, deeper shelf water.

Diel variation in catch rates was not observed here. This may be due to the relatively deep water fished compared with the shallow nearshore locations where such differences have been consistently observed (Keats 1990; Keats and Steele 1992; Methven and Bajdik 1994). Diel behavior patterns among age 0 and 1 juvenile cod may therefore be restricted to these shallow nearshore habitats. Alternatively, by the December–January period, juvenile cod may have adopted their winter behavior which includes reduced activity and food consumption (Brown et al. 1989) and unchanging patterns throughout the day (Gregory and Anderson 1996).

Annual differences in mean catch rate of age 2 and 3 cod indicated that year-class strength significantly decreased between 1989 and 1991. There appeared to be a trend towards increasing year-class strength each year since 1991, but the differences in mean catch rate of age 0 and 1 cod in the analysis were not significant among years. Comparisons of mean catch rates of age 0 and 1 cod in 1992 are constrained by the lack of a codend liner in the trawl, the presence of which would have improved the catchability of smaller juvenile cod.

Annual mean catch rates at age 0 were lower than mean catch rate at age 1 in all years. This result demonstrates a catchability bias for age 0 cod in our surveys. Such a bias may result from low selectivity by the trawl for age 0 cod or from age 0 cod being distributed in untrawlable areas where we could not trawl. Historically, high catch rates of juvenile cod have been reported in the nearshore environment, <10 m water depth, of Newfoundland (Lear et al. 1980; Methven and Bajdik 1994; Schneider et al. 1997). As our shallowest tow depth was approximately 60 m, it may be that age 0 cod were distributed more shoreward of our trawling locations than age 1 cod. However, Anderson and Dalley (1995) demonstrated, for selected sites, that the abundances of both age 0 and 1 cod were relatively high from the nearshore out to approximately 40 m depth, inclusive. In the present study, a low number of sets did catch higher numbers of age 0 than age 1 cod and these high catch rates tended to occur at the same locations each year. This result indicated that age 0 cod did occur abundantly at water depths deeper than the nearshore and that the trawl could catch these small cod when present. Together, these results suggest that the low catchability of age 0 cod

© 1997 NRC Canada

Fig. 4. Distribution of age 1 juvenile cod sampled during demersal trawl surveys carried out in inshore/offshore northeast Newfoundland, 1992–1994. The expanding symbols represent a linear scale based on catches per 30-min tow. Crosses represent zero catches.

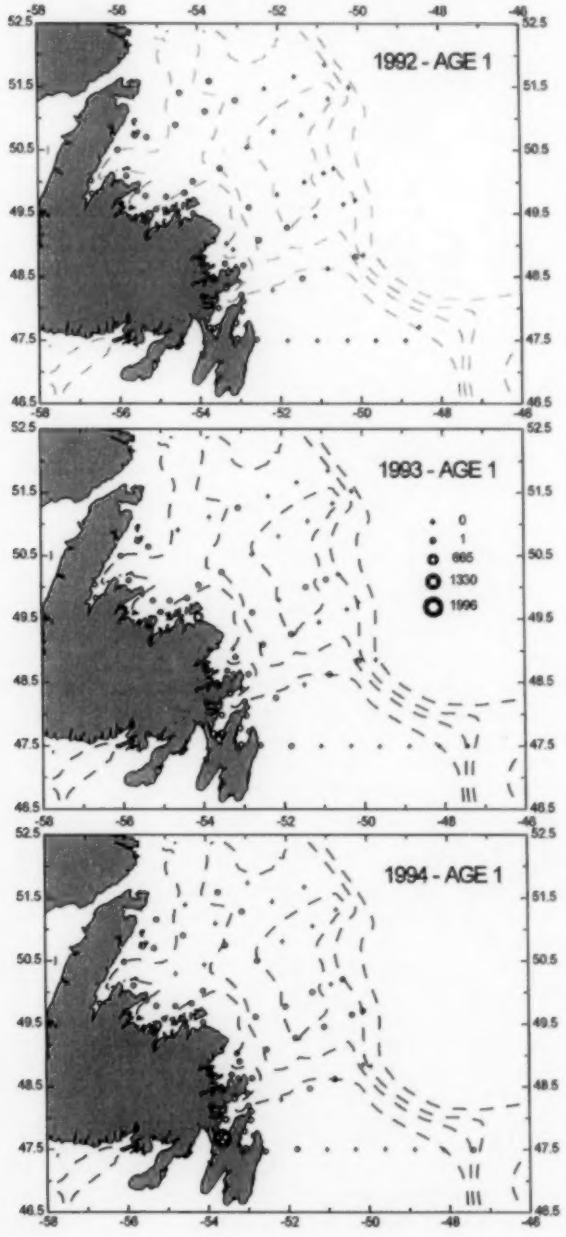
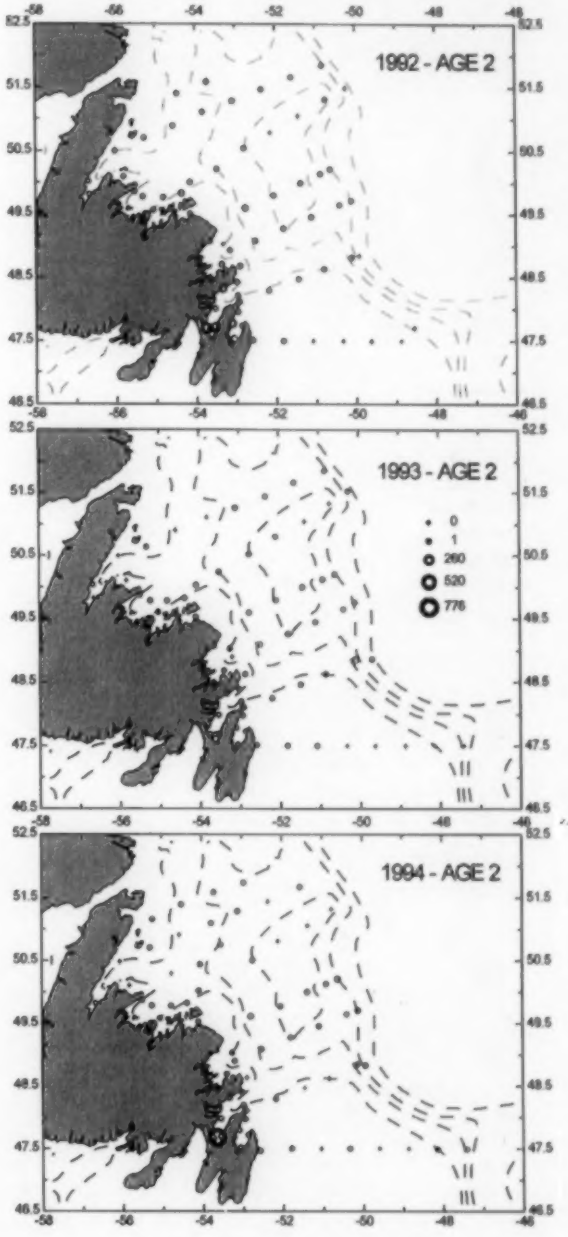


Fig. 5. Distribution of age 2 juvenile cod sampled during demersal trawl surveys carried out in inshore/offshore northeast Newfoundland, 1992–1994. The expanding symbols represent a linear scale based on catches per 30-min tow. Crosses represent zero catches.



arose because they were also distributed in untrawlable areas, rather than being distributed exclusively at shallower depths.

Survival of newly demersal juvenile cod has been linked to substrate types, rougher bottom offering reduced predation risk (Lough et al. 1989; Tupper and Boutilier 1995). Age 0 cod readily seek shelter among cobble when threatened (Gotceitas and Brown 1993; Gotceitas et al. 1995) and may evade capture by trawls. Extremely rough bottoms are untrawlable and are prevalent throughout much of the inshore area. Any abundance indices for juvenile cod must take into account the extent of these areas and their relative utilization by juveniles. Recent inshore observations made from submersibles show that juvenile cod do in fact utilize such untrawlable habitats (Gregory and Anderson 1996).

© 1997 NRC Canada

Fig. 6. Distribution of age 3 juvenile cod sampled during demersal trawl surveys carried out in inshore/offshore northeast Newfoundland, 1992–1994. The expanding symbols represent a linear scale based on catches per 30-min tow. Crosses represent zero catches.

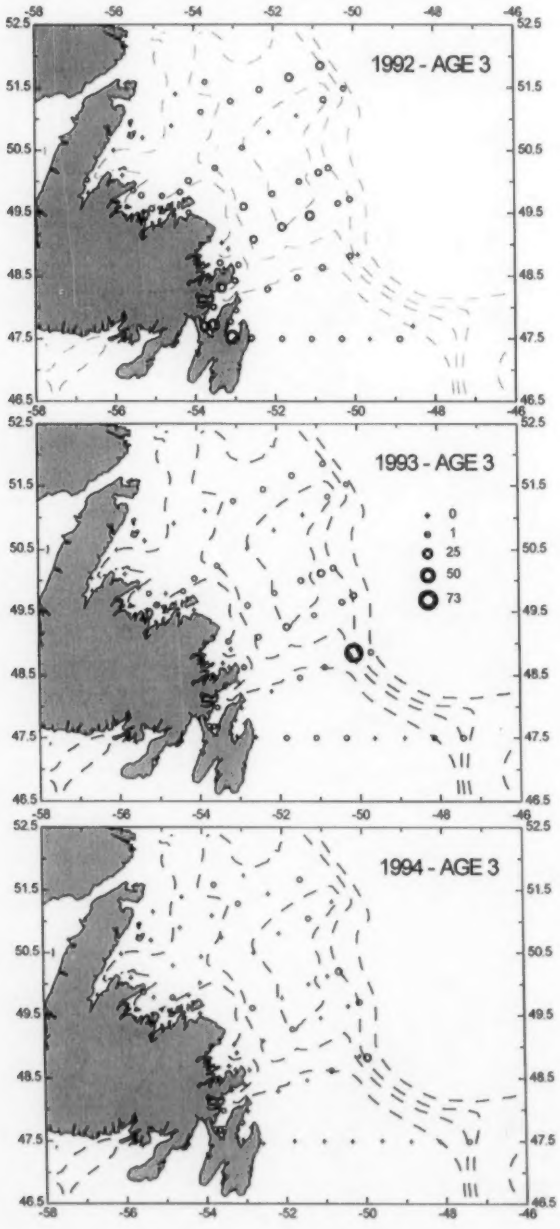
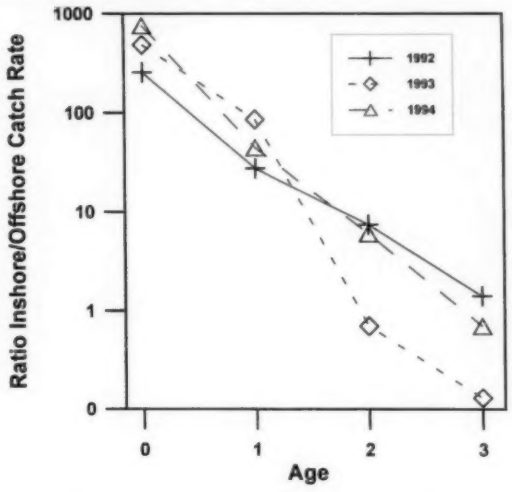


Fig. 7. Ratio of mean inshore to offshore catch rate for each age group of juvenile cod taken in demersal trawl surveys carried out in inshore/offshore northeast Newfoundland, 1992–1994.



It is difficult to compare the distributions of age 0 cod in our study with historical observations. Inshore, the only sampling carried out historically was in the very nearshore, i.e., <10 m water depth, using a beach seine (Lear et al. 1980). However, our inshore observations showing that age 0 cod were more abundant in area 3L than in 3K (two of the three years) and that age 1 cod were more abundant in 3L in all three years are consistent with historical offshore data which indicated that abundance of youngest juveniles increased from north to south (Bulatova 1962, 1963, 1971, 1980).

Age 0 cod were caught historically in offshore areas off southern Labrador and northeast Newfoundland (Bulatova 1962, 1963, 1971). These observations were made using a trawl that had low catchability for age 0 cod relative to older ages (Bulatova 1962). A feeding study of larger cod (Bogstad et al. 1994) also substantiated that age 0 cod occurred in the offshore. These offshore occurrences, coupled with the almost exclusive inshore distribution of age 0 cod in the present study (a total of only three age 0 cod were taken in the offshore area in the three surveys), suggest that offshore distribution of demersal age 0 cod may have been more extensive historically, when the stock was healthier. Settlement of juveniles probably occurs later in the relatively deep, high-latitude shelves than in the inshore areas (Methven and Bajdik 1994). It is expected, however, that settlement should have occurred by the time of our early winter surveys.

The relative contributions of inshore versus offshore spawning in the propagation of this stock complex have not been determined. Bulatova (1971) assumed that age 0 demersal fish collected historically offshore in 3KL were the progeny of cod that spawned on offshore banks, and egg and larval drift models (Helbig et al. 1992; Davidson and deYoung 1995; Pepin and Helbig 1997) support the premise that progeny from this area mostly remain offshore. deYoung and Rose (1993) hypothesized that spawning in this area contributed the most to the production of the 2J3KL northern cod stock. Hutchings et al. (1994) concluded, however, that inshore spawning may contribute more to cod recruitment than previously believed. Anderson et al. (1995) presented evidence from pelagic juvenile distributions that offshore spawning products do not drift to the inshore, and Anderson and Dalley (1997) concluded that inshore distributions of pelagic juvenile cod reflect inshore spawning. In 1981, a year

© 1997 NRC Canada

Table 5. Mean catch rate (no. of cod·30-min tow^{-1}) of demersal juvenile cod, by age, inshore and offshore 3K and 3L during demersal surveys carried out in 1992–1994 (standard deviation of mean catch rate shown in parentheses).

	3K		3L	
Year	Inshore	Offshore	Inshore	Offshore
Age 0				
1992	0.090 (1.73)	0.00	11.53 (23.17)	0.08 (0.29)
1993	19.70 (54.00)	0.05 (0.22)	11.24 (20.64)	0.00
1994	22.56 (45.67)	0.07 (0.27)	79.77 (207.19)	0.08 (0.28)
Age 1				
1992	12.20 (11.84)	1.60 (2.90)	47.18 (75.40)	0.50 (1.17)
1993	70.80 (198.03)	0.81 (1.83)	91.24 (132.29)	1.20 (2.11)
1994	8.00 (6.36)	4.07 (8.76)	203.77 (483.29)	0.92 (1.44)
Age 2				
1992	17.30 (14.17)	9.32 (15.32)	75.71 (102.37)	3.08 (5.52)
1993	6.80 (7.38)	6.71 (6.81)	4.24 (3.65)	9.07 (18.66)
1994	4.11 (3.44)	8.15 (15.70)	58.77 (185.27)	3.62 (5.88)
Age 3				
1992	2.00 (1.89)	6.44 (6.76)	11.00 (15.23)	3.75 (3.96)
1993	0.70 (1.57)	3.10 (3.95)	0.41 (0.80)	7.40 (18.38)
1994	0.44 (1.01)	1.15 (2.63)	1.00 (2.67)	1.39 (4.41)

that produced a relatively strong year-class, pelagic 0-group cod occurred extensively inshore and offshore, but the inshore was estimated to have accounted for only 10% of the pelagic juvenile cod sampled in the fall (Anderson et al. 1995). The most extensive offshore distribution of pelagic 0-group cod in recent years was observed in 1994 (Anderson and Dalley 1997). Results from the present study indicated that these age 0 pelagic juveniles did not result in increased abundance of settled demersal juveniles in the offshore area by early winter. A corresponding increase in demersal 0-group juveniles was observed only at the head of Trinity Bay. If age 0 demersal juveniles collected in the inshore were derived predominantly from inshore spawning, as predicted from the models, and supported by pelagic 0-group distributions, the offshore contribution to overall recruitment was extremely small from 1992 to 1994. The lack of age 0 demersal cod in the offshore is a result of spawning failure of the offshore components of the stock complex in recent years and indicates that the inshore will play a major role during the rebuilding stage. A wider distribution of age 0 demersal cod on the shelf in the future may result from a return of successful offshore spawning.

Demersal trawl surveys are a useful tool for monitoring relative strength of prerecruit age groups of cod. However, to appropriately assess the relative strength of prerecruits of northern cod as the stock rebuilds, it would be necessary to include inshore areas not traditionally covered during annual groundfish resource surveys (Bishop et al. 1994). High proportions of juvenile cod, particularly ages 0–2, occupy the inshore. Since large numbers of cod (particularly ages 0–1) occur shoreward of inshore areas surveyed here (Lear et al. 1980; Schneider et al. 1997), indices from the nearshore should also be considered. Potential biases in the index could be minimized by determining extent and relative utilization of untrawlable areas by juvenile cod.

Acknowledgements

We thank the officers, particularly Captain H. Green, and fishing crew, particularly G. Antle, of the *Wilfred Templeman* for their enthusiasm, cooperation, and expertise in carrying out the surveys. Technical staff that participated at sea, particularly E. McDonald, are thanked for their assistance in carrying out the sampling program. D. Davis is thanked for data processing. We thank J. Carscadden, E. Dawe, B. Nakashima, B. Gregory, and two anonymous reviewers for constructive comments on the manuscript. The work was supported by DFO's Northern Cod Sciences Program.

References

Anderson, J.T. 1993. Distributions of juvenile cod in NAFO Divisions 2J3KL during fall, 1981–1992, in relation to bathymetry and bottom temperatures. NAFO SCR Doc. 93/68.

Anderson, J.T., and Dalley, E.L. 1995. Nearshore distribution and abundance of juvenile Atlantic cod (*Gadus morhua*) at two sites in coastal waters of Newfoundland. Nfld. Regional Groundfish Assess. WP95/19.

Anderson, J.T., and Dalley, E.L. 1997. Spawning and year-class strength of northern cod (*Gadus morhua*) as measured by pelagic juvenile cod surveys, 1991–1994. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Anderson, J.T., Dalley, E.L., and Carscadden, J.E. 1995. Abundance and distribution of pelagic 0-group cod (*Gadus morhua*) in Newfoundland waters: inshore versus offshore. Can. J. Fish. Aquat. Sci. **52**: 115–125.

Assthorsson, O.S., Gislason, A., and Gudmundsdottir, A. 1994. Distribution, abundance, and length of pelagic juvenile cod in Icelandic waters in relation to environmental conditions. ICES Mar. Sci. Symp. **198**: 529–541.

Bishop, C.A., Anderson, J., Dalley, E., Davis, M.B., Murphy, E.F., Rose, G.A., Stansbury, D.E., Taggart, C., and Winters, G. 1994. An assessment of the cod stock in NAFO Divisions 2J+3KL. NAFO SCR Doc. 94/40, Ser. No. N2410.

© 1997 NRC Canada

Bogstad, B., Lilly, G.R., Mehl, S., Palsson, O.K., and Stefansson, G. 1994. Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland and eastern Newfoundland). ICES Mar. Sci. Symp. **198**: 576–599.

Brown, J.A., Pepin, P., Methven, D.A., and Somerton, D.C. 1989. The feeding, growth and behavior of juvenile cod, *Gadus morhua* L., in cold environments. J. Fish Biol. **35**: 373–380.

Bulatova, A.Y. 1962. Some data on distribution of young cod and haddock off Labrador and Newfoundland. ICNAF Redbook 1962, Part III. pp. 69–78.

Bulatova, A.Y. 1963. Results of determining the abundance of young of commercial fishes in the Labrador and Newfoundland areas, December, 1962/January, 1963. ICNAF (1963) Doc. 61, Ser. No. 1132.

Bulatova, A.Y. 1970. Abundance of young cod in the waters off Newfoundland. ICNAF Redbook 1970, Part III. pp. 56–64.

Bulatova, A.Y. 1971. Estimation of young cod in the Labrador and Newfoundland areas in 1961–67. Proc. Polar Res. Inst. Mar. Fish. Oceanogr. **23**: 262–278. (Fish. Res. Board Can. Transl. Ser. No. 1917)

Bulatova, A.Y. 1980. Abundance of young cod on the Labrador–Newfoundland Shelf in March–June 1979. NAFO SCR. Doc. 80/120, Ser. No. N189.

Bulatova, A.Y. 1990. Assessment of the cod stock in Div. 3NO and Div. 3KL from the 1989 trawl-acoustic survey. NAFO SCR. Doc. 90/05, Ser. No. N1716.

Campana, S.E., Frank, K.T., Hurley, P.C.F., Koeller, P.A., Page, F.H., and Smith, P.C. 1989. Survival and abundance of young Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) as indicators of year-class strength. Can. J. Fish. Aquat. Sci. **46**(Suppl. 1): 171–182.

Clark, D.S., and Green, J.M. 1990. Activity and movement patterns of juvenile Atlantic cod, *Gadus morhua*, in Conception Bay, Newfoundland as determined by sonic telemetry. Can. J. Zool. **68**: 1434–1442.

Davidson, F.J.M., and deYoung, B. 1995. Modeling advection of cod eggs and larvae on the Newfoundland Shelf. Fish. Oceanogr. **4**(1): 33–51.

deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. **50**: 2729–2741.

Engas, A., and Godo, O.R. 1989. Escape of fish under the fishing line of a Norwegian fishing trawl and its influence on survey results. J. Cons. Int. Explor. Mer, **45**: 269–276.

Goddard, S.V., Kao, M.H., and Fletcher, G.L. 1992. Antifreeze production, freeze resistance, and overwintering of juvenile northern cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **49**: 516–522.

Godo, O.R., and Walsh, S.J. 1992. Escapement of fish during bottom trawl sampling — implications for resource assessment. Fish. Res. **13**: 281–292.

Gotceitas, V., and Brown, J.A. 1993. Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia, **93**: 31–37.

Gotceitas, V., Fraser, S., and Brown, J.A. 1995. Habitat use by juvenile Atlantic cod (*Gadus morhua* L.) in the presence of an actively foraging and non-foraging predator.

Gregory, R.S., and Anderson, J.T. 1996. Substrate selection and use of protected cover by juvenile Atlantic cod (*Gadus morhua*) in inshore waters of Newfoundland. Mar. Ecol. Prog. Ser. (In press)

Helbig, J., Mertz, G., and Pepin, P. 1992. Environmental influences on the recruitment of Newfoundland/Labrador cod. Fish. Oceanogr. **1**: 39–56.

Hutchings, J.A., Myers, R.A., and Lilly, G.R. 1994. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2457–2467.

Ings, D.W., Schneider, D.C., and Methven, D.A. 1997. Detection of a recruitment signal in juvenile Atlantic cod (*Gadus morhua*) in coastal nursery areas. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Jakupsstovu, S.H., and Reinert, J. 1994. Fluctuations in the Faroe Plateau cod stock. ICES Mar. Sci. Symp. **198**: 194–211.

Keats, D.W. 1990. A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. J. Exp. Mar. Biol. Ecol. **139**: 167–173.

Keats, D.W., and Steele, D.H. 1992. Diurnal feeding of juvenile cod (*Gadus morhua*) which migrate into shallow water at night in Eastern Newfoundland. J. Northwest Atl. Fish. Sci. **13**: 7–14.

Keats, D.W., South, G.R., and Steele, D.H. 1987. The role of macroalgae in the distribution and feeding of juvenile codfish (*Gadus morhua* L.) in inshore waters off eastern Newfoundland. Can. J. Zool. **65**: 49–53.

Koeller, P., McCallum, B., Swain, D., Strong, M., Archambault, D., and Walsh, S.J. 1994. Accuracy and precision of Scanmar data recorded on Canadian groundfish surveys. Can. Tech. Rep. Fish. Aquat. Sci. No. 1983.

Kuzmin, S.A., and Tevs, I.I. 1991. Distribution of various age-groups of cod in the Newfoundland area by the 1988–1990 survey results. NAFO SCR. Doc. 91/124, Ser. No. N2017.

Lear, W.H., Fleming, A.M., and Wells, R. 1980. Results of small cod surveys in eastern Newfoundland during 1959–64. NAFO SCR. Doc. 80/144, Ser. No. N218.

Lough, R.G., Valentine, P.C., Potter, D.C., Auditore, P.J., Bolz, G.R., Neilson, J.D., and Perry, R.I. 1989. Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Mar. Ecol. Prog. Ser. **56**: 1–12.

Mehl, S. 1989. The Northeast Arctic cod stock's consumption of commercially exploited prey species in 1984–1986. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **188**: 185–205.

Methven, D.A., and Bajdik, C. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 78–90.

Pepin, P., and Helbig, J.A. 1997. Distribution and drift of cod eggs and larvae on the northeast Newfoundland Shelf. Can. J. Fish. Aquat. Sci. **54**. (In press)

SAS Institute Inc. 1989. SAS/STAT user's guide, release 6.03 edition SAS Institute Inc., Cary, N.C.

Schneider, D.C., Dalley, E.L., and Methven, D.A. 1997. Geographic contraction in juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Sissenwine, M.P. 1984. Why do fish populations vary? *In* Exploitation of marine communities. *Edited by* R.M. May. Dahlem Workshop Reports, Life Sciences Research Report 32. Springer-Verlag, New York. pp. 59–94.

Sundby, S., Bjorke, H., Soldal, A.V., and Olsen, S. 1989. Mortality rates during the early life stages and year-class strength of northeast Arctic cod (*Gadus morhua*). Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **191**: 351–358.

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

Tupper, M., and Boutilier, R.G. 1995. Effects of habitat on settlement, growth and postsettlement survival of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **52**: 1834–1841.

© 1997 NRC Canada

Evidence for inshore spawning of northern Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, 1991–1993

R. Kent Smedbol and J.S. Wroblewski

Abstract: Northern Atlantic cod (*Gadus morhua*) were found to spawn in Trinity Bay, Newfoundland, during the early summer each year from 1991 to 1993. Prior to this study, only indirect evidence of inshore spawning by cod along the northeast coast of Newfoundland existed. We observed (1) the progressive maturation of Trinity Bay cod from ripening to spawning and spent condition, (2) a spawning aggregation of cod in Trinity Bay, and (3) the presence of recently spawned cod eggs (≤10 d old) in the bay. We estimate that peak spawning occurred in the bay from mid-June to mid-July for the years 1991–1993. This spawning was delayed relative to estimated times of offshore spawning by northern cod. A simple model is proposed to explain this delay based upon the subzero temperatures that bay cod experience during the winter. Model predictions of oocyte development times for female bay cod were in phase with observed spawning times.

Résumé : Nous avons constaté que, chaque année de 1991 à 1993, la morue du Nord (*Gadus morhua*) a frayé au début de l'été dans la baie de la Trinité, à Terre-Neuve. Avant la présente étude, on ne disposait que de preuves indirectes de la ponte de la morue dans la zone côtière au nord-est de Terre-Neuve. Nous avons observé 1) l'évolution de la morue de la baie de la Trinité, depuis la phase de l'élaboration génitale jusqu'à la fraye et à la condition de poisson vide, 2) un rassemblement de morues en train de frayer dans la baie de la Trinité et 3) la présence dans la baie d'oeufs de morue fraîchement pondus (≤10 jours). Nous estimons que la période de fraye a culminé dans la baie de la mi-juin à la mi-juillet dans les années 1991–1993. Cette fraye était tardive par rapport aux estimations de la ponte de la morue du Nord au large. Nous proposons un modèle simple pour expliquer ce décalage, qui se base sur les températures inférieures à zéro auxquelles sont soumises les morues de la baie au cours de l'hiver. Les prédictions fournies par le modèle quant aux périodes de développement des ovocytes chez les morues femelles de la baie étaient compatibles avec les périodes de fraye observées.
[Traduit par la Rédaction]

Introduction

Present models of spawning by Atlantic cod (*Gadus morhua*) in Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J3KL describe the reproductive behaviour of fish that congregate near the edge of the continental shelf (Lear and Parsons 1993). Spawning generally occurs in the spring, near Hamilton Bank off southeastern Labrador, and over Funk Island and Belle Isle banks off the northeast coast of Newfoundland (Templeman and May 1965; Serebryakov 1967; Templeman 1979; Fitzpatrick and Miller 1979). Hutchings et al. (1993) described cod in spawning condition dispersed over broad regions of the continental shelf and in inshore regions. Reports of cod in spawning condition in major Newfoundland bays are not new (Neilsen 1894, 1895; Graham 1922). Hutchings et al. (1993) presented data from research gillnet surveys on the presence of cod in spawning condition in Trinity Bay during the spring in the years 1967–68. Indirect evidence for inshore spawning also arises from a study by Anderson et al. (1993) who concluded that it was unlikely that 0-group cod sampled in 1985 in Trinity Bay were advected from offshore spawning locations.

Inshore spawning has been reported for the Scotian Shelf and the coast of Norway. McKenzie (1940) provided documentation of autumn spawning in Halifax Harbour, Nova Scotia. Cod spawn annually in the fjords of Norway (Trout 1957; Jakobsen 1987; Godø and Sunnanå 1984). Apparently, inshore spawning is part of the reproductive biology of Atlantic cod. Therefore, spawning would be expected to occur in Newfoundland inshore waters as well.

Recent sonic tracking studies have shown that some adult cod overwinter in the Random Island area of Trinity Bay (Wroblewski et al. 1994) instead of migrating to offshore regions during the autumn (Templeman 1974, 1979; Lear 1984). These observations were complemented by a physiological study of cod in the Random Island region by Goddard et al. (1994) who used plasma antifreeze glycoprotein levels and tag–recapture data to demonstrate that some cod overwinter in subzero inshore waters. The question then arises, where and when do these bay cod spawn? This study provides direct evidence of spawning in Trinity Bay, and discusses the environmental factors that may influence the timing of inshore spawning.

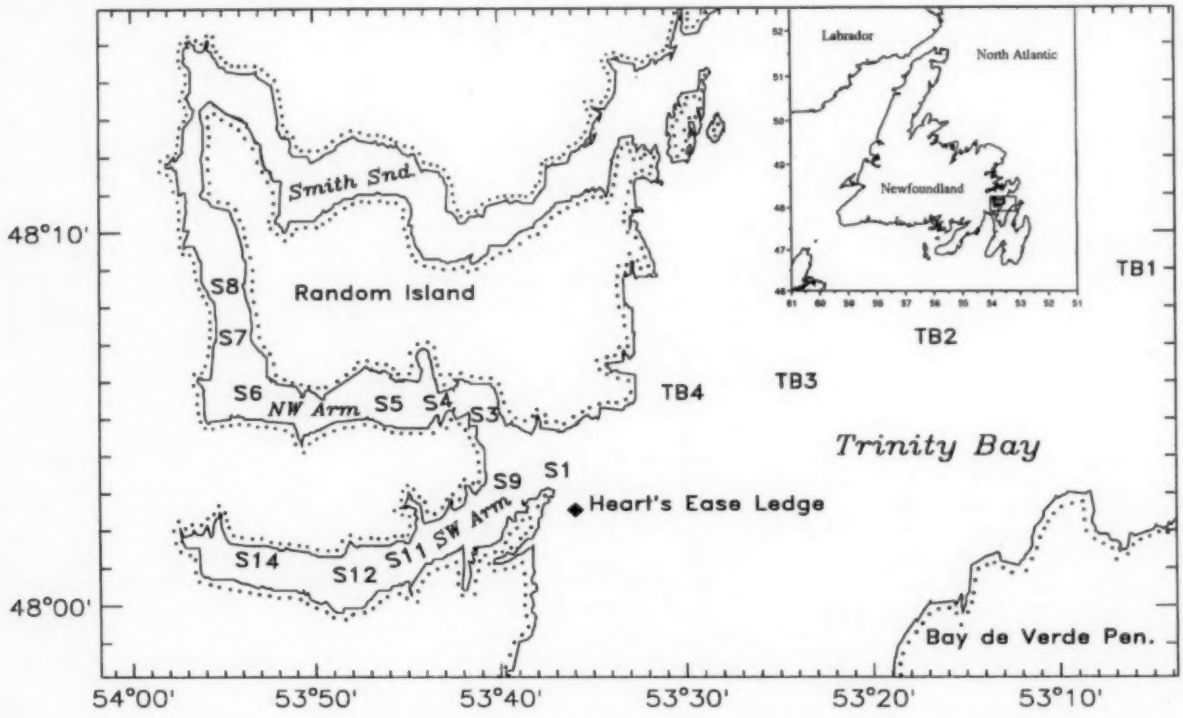
Given that cod are known to spawn on the Northeast Newfoundland Shelf in waters near 3°C (Templeman 1979; Rose 1993), we wished to test the hypothesis that inshore spawning is initiated when waters warm above 0°C. In Trinity Bay the

Received January 11, 1995. Accepted August 5, 1995.
J13226

R.K. Smedbol and J.S. Wroblewski. Fisheries Oceanography Group, Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, NF A1B 3X7, Canada.

© 1997 NRC Canada

Fig. 1. Random Island study region. Stations S1–S14 mark the position of ichthyoplankton survey stations in 1991 and 1993. Stations TB1–TB4 were also occupied in 1993. Experimental fishing took place near station S14 on 22 April 1993. The diamond marks the location where spawning cod were found in July 1993.



region of the water column beneath the seasonal thermocline remains subzero year-round; therefore, shoal areas that intersected the 0°C isotherm were of interest. We also wished to test the hypothesis that the cold temperature history of cod overwintering in the bay would delay the initiation of spawning relative to that by cod overwintering offshore in warmer waters.

Materials and methods

Sampling of commercial catches from Random Island, Trinity Bay, 1991–1992

Commercial landings of cod in the Random Island region of Trinity Bay (Fig. 1) were sampled at dockside from May to September of 1991 and 1992 (Smedbol 1994) to document the presence of spawning cod in Trinity Bay and to define the timing of spawning. Data were also derived from experimental fishing in Southwest Arm near Random Island (Fig. 1) on 22 April 1993. A fleet of five gill nets was deployed from the chartered longliner C.F.V. *Northern Quest*. Each net was 91.5 m (50 fa) in length and 3 m (1.7 fa) in width, with 13.8-cm (5.5-in.) mesh.

Variables recorded in both data sets included date of capture, length, weight, sex, and gonadal condition. Length was recorded as fork length measurements (±1 mm) and weight as whole wet body weight (±50 g). State of sexual maturity was recorded following the criteria of Morrison (1990), who defined females to be in spawning condition (stage 2) if translucent (hydrated) eggs were present in the ovaries. Hydrated eggs will normally be released in about 3 d (Kjesbu et al. 1990). Morrison (1990) considered males to be in spawning condition (stage 2) if their testes and efferent ducts were white. Females were recorded as spent if their ovaries were shrunken, soft, and flabby with whitish cast. Males were spent if their proximal testes were white and flabby. The peak and duration of probable spawning were estimated from the proportion of catch in spawning condition.

Hydroacoustic survey in the Random Island area of Trinity Bay, 1993

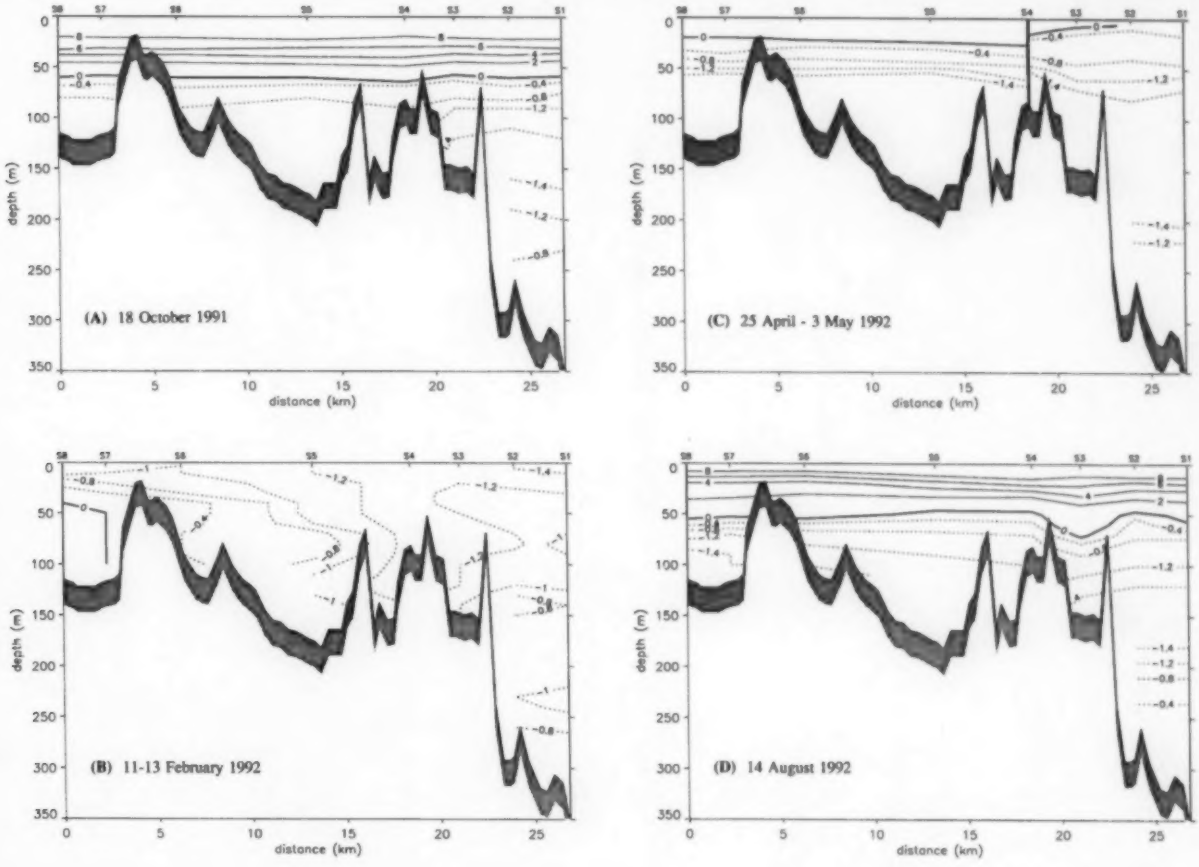
The analysis of cod caught commercially in 1991–1992 was used to plan a hydroacoustic survey in 1993. In both 1991 and 1992, the highest proportion of stage 2 (ripe/spawning) fish was caught in June. Therefore, the timing of the survey was set for late June and early July.

Possible spawning locations were predicted according to several criteria. Offshore spawning of cod occurs in water temperatures near 3°C (Templeman 1979; Rose 1993). Also, adult cod held in captivity at the Marine Science Research Laboratory of Memorial University spawn when water temperatures warm to approximately 2°C (Leader 1994). Therefore, the survey focused on inshore areas where water temperatures were >0°C.

The survey for aggregations of cod was conducted from 28 June to 9 July 1993 aboard the C.R.V. *Shamook*. Data from a Biosonics No. 105 portable sounder with a single beam transducer (120 kHz) were logged using a Biosonics No. 115 portable chart recorder. A Simrad EQ100 (38 kHz) was used to sample depths >100 m. Temperature profiles along the survey transect (Smedbol 1994) were recorded using a Sea-bird Electronics CTD (model SBE 19-03). Cod were sampled from spawning aggregations using Norwegian jiggers.

© 1997 NRC Canada

Fig. 2. Temperature sections of Northwest Arm, Trinity Bay (after Wroblewski et al. 1993). Sections have been selected that show the seasonal temperature variation. Data from station S4 were used in the estimates of egg and gonad development times.



For each individual fish the length, weight, sex, and gonad condition were recorded in the same manner as the commercially caught cod (see above). Blood samples were collected for the determination of plasma antifreeze glycoprotein levels (for methods, see Goddard et al. 1992). Tissue samples were taken for genetic analysis, following the methods for mtDNA sequencing of Carr and Marshall (1991).

Ichthyoplankton surveys in the Random Island area of Trinity Bay, 1991 and 1993

During May–September 1991, ichthyoplankton samples were collected at 10 stations in Northwest Arm and Southwest Arm (Fig. 1) at roughly monthly intervals. Samples were collected again from these stations during late June – early July 1993, together with samples from a transect across Trinity Bay (Fig. 1). Ichthyoplankton samples were also obtained near an aggregation of spawning cod found near Heart's Ease Ledge on 3–6 July 1993.

Plankton sampling was undertaken with a 1-m ring net with 333-μm mesh and a 333-μm cod end. Oblique tows were carried out with elapsed times of 7–25 min, and a tow velocity of 0.5–1.0 $m \cdot s^{-1}$ (1–2 kn) with payout and retrieval rates of approximately 0.5 $m \cdot s^{-1}$. Maximum tow depth was 45 m. Volumes filtered were calculated using a General Oceanics flowmeter (model GEO2030R). Plankton samples were fixed in a 4% buffered formalin–seawater solution.

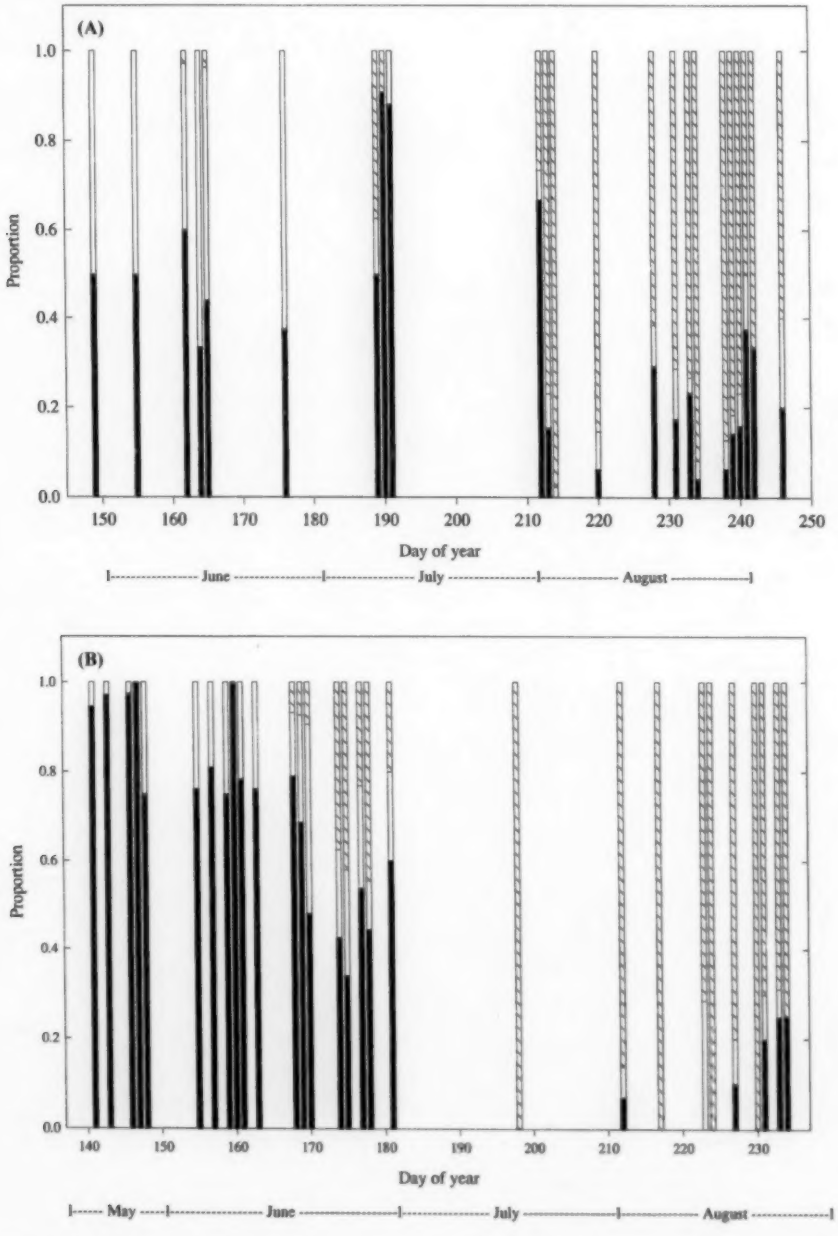
Cod eggs were identified to stage of development following the criteria of Page and Frank (1989). Date of spawning was back-calculated using the relationship of egg stage duration to incubation temperature reported in table 9 of Page and Frank (1989). The age reported for eggs at each station was calculated using the oldest staged eggs collected at the site. Reported age therefore represents a maximum possible age for the eggs from each station. Some eggs in the sample may be younger.

Temperatures used in aging the eggs collected in 1991 were from a 1991–1992 time series recorded in Northwest Arm (Wroblewski et al. 1993) (Fig. 2). There was little areal variation in the temperature profiles of all the stations at a given time of year. Therefore, the vertical structure found at any one station at a particular time was representative of all stations in the study area at that time. The temperatures recorded at Station S4 (Fig. 1 and 2) were used in the aging calculations because this station was sampled more frequently than the others. Temperature profiles were recorded at roughly monthly intervals. For each month the mean temperature from the surface to the 0°C isotherm was calculated. This isotherm varied in depth from 40 to 80 m during the summer. Since all tows did not exceed 45 m in depth, this depth-averaged temperature was considered a reasonable approximation of the temperatures to which cod eggs were exposed.

Early-stage cod eggs cannot be distinguished from early-stage haddock (*Melanogrammus aeglefinus*) and witch flounder (*Glyptocephalus cynoglossus*) eggs (Fahay 1983). Such eggs are therefore termed "chw". Currently, haddock and witch flounder are very rare in Trinity Bay relative to cod (Bowering et al. 1993; Villagarcia

© 1997 NRC Canada

Fig. 3. Gonadal condition of adult Atlantic cod sampled from commercial catches in the Random Island area of Trinity Bay during (A) 1991 (n = 828) and (B) 1992 (n = 763). The bars represent the number of adult cod at each stage of maturity (solid bars, ripening; open bars, ripe/spawning; hatched bars, spent) at each sampling date. Only those dates when $n \geq 5$ are plotted (see Table 1).



1995). All chw eggs thus were assumed to be cod eggs, even though some unknown proportion may have belonged to the other two species.

Results

Spawning cod in commercial catches, 1991–1992

A total of 2656 cod (of which 1591 were adults) were sampled from the commercial catches made in the Random Island area of Trinity Bay in 1991 and 1992. A progression in the reproductive cycle of adult cod was observed during the spring and summer (Fig. 3; Table 1). In May, the gonads of most adult fish were ripening. The greatest proportion of ripe fish in the sample appeared during the month of June (days 145–175). In August and September (days 213–247), most of the adults in the sample were spent (Fig. 3). These samples in

© 1997 NRC Canada

Table 1. Number of Atlantic cod sampled from the Random Island commercial fishery in 1991 and 1992 to determine gonadal condition (see Fig. 3).

1991 Day of year	*n*	1992 Day of year	*n*
149	12	141	18
155	6	143	35
162	35	146	154
164	21	147	10
165	82	148	8
176	8	155	21
189	8	157	21
190	11	159	12
191	17	160	10
212	15	161	37
213	13	163	21
214	43	168	43
220	48	169	67
228	65	170	52
231	115	174	40
233	30	175	50
234	73	177	13
238	63	178	9
239	49	181	10
240	82	198	6
241	16	212	29
242	6	217	11
246	10	223	14
		224	5
		227	10
		230	11
		231	10
		233	16
		234	20

late summer may have included cod that migrated to the coast after spawning earlier on the coastal shelf.

The 23 adult fish caught by experimental fishing on 22 April 1993 were all stage 1 (ripening) or stage 2 (in spawning condition). These fish were caught near the shore at depths <35 m, in shallow, sub-zero temperature seawater.

A maximum likelihood probit analysis was used to calculate the length at 50% maturity for the commercial catch data sets. The PROC PROBIT procedure of SAS statistical software (SAS Institute, Inc. 1989) was employed. The M_{50} for females was 34.26 ± 12.21 cm SD in 1991 and 47.52 ± 9.99 cm in 1992. Male M_{50} was 41.48 ± 8.89 cm in 1991 and 45.18 ± 8.32 cm in 1992. Combined 1991 and 1992 values were 47.54 ± 10.32 cm for females and 45.17 ± 8.30 cm for males.

An aggregation of spawning cod over Heart's Ease Ledge, July 1993

An aggregation of spawning cod was discovered 1.8 km off Gooseberry Cove, Trinity Bay, over Heart's Ease Ledge shoal (Fig. 1) on 2 July 1993. The fish were concentrated over the shallowest part of the shoal, and the school exhibited a very discrete boundary. The aggregation was on the order of 300–400 m in length along its north–south axis. Many of the cod in the aggregation were actively spawning; individual males had running milt, and females were extruding hydrated eggs as they were brought aboard the research vessel. Both mature and immature cod were present. All fish sampled from this assemblage were caught at depths <45 m. Water column temperature ranged from 8°C at the surface to 1°C at the bottom (Fig. 4). The spawning aggregation was located primarily in 1–4°C waters (Fig. 4).

Fig. 4. Temperature profile taken within the aggregation of Atlantic cod detected over Heart's Ease Ledge, Trinity Bay, on 2 July 1993 at 16:45 NDST. The depths at which the majority of cod were detected with a Simrad EQ100 (38 kHz) echosounder are indicated. Bottom depth was 45 m.

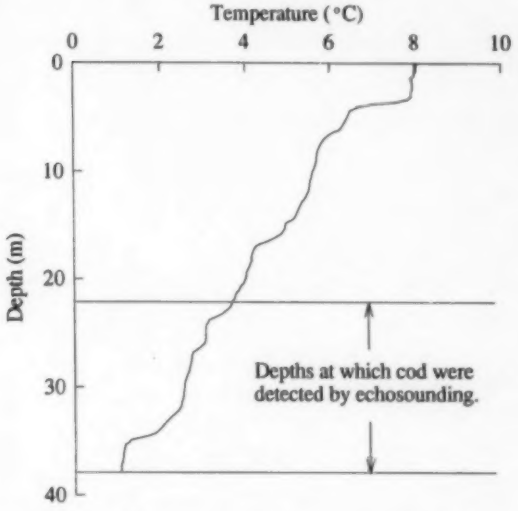
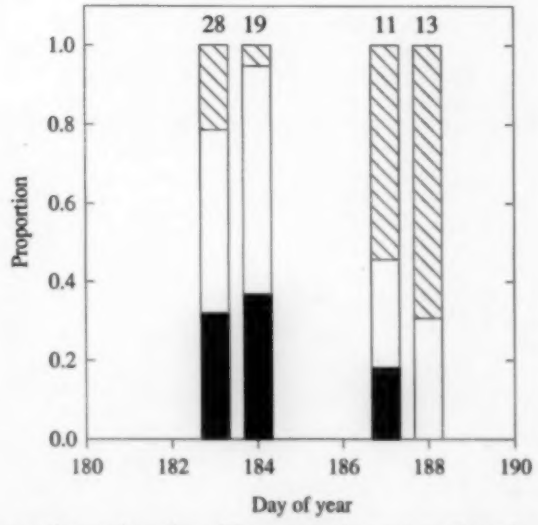


Fig. 5. Gonadal condition of adult Atlantic cod sampled from the spawning aggregation over Heart's Ease Ledge, Trinity Bay, from 2 to 7 July 1993 (n = 71).



© 1997 NRC Canada

Table 2. Summary of cod egg abundances (eggs·1000 m^{-3}; upper value) and ages (d; lower value) from ichthyoplankton surveys in the Random Island area of Trinity Bay during the summers of 1991 and 1993 (the egg ages are for the oldest eggs in the sample).

Station	27–28 May 1991	17–18 June 1991	17–18 July 1991	14–15 Aug. 1991	16–17 Sept. 1991	29–30 June 1993
S1	0.01	5.7	2.8	17.1	0	28.4
	28	16	≤10	9	—	≤10
S3	27.3	8.9	4.9	19.2	0	45.1
	28	22	17	15	—	≤10
S5	5.0	5.9	7.5	36.8	0	67.1
	30	16	17	15	—	≤10
S6	—	—	101.2	80.8	0	349.2
	—	—	17	15	—	≤10
S7	0	4.4	—	—	—	75.7
	—	16	—	—	—	12
S8	2.7	13.6	91.1	124.0	0	81.6
	28	22	17	15	—	≤10
S9	35.7	91.1	17.4	10.0	0	—
	28	16	17	9	—	—
S11	—	—	—	—	—	10.9
	—	—	—	—	—	≤10
S12	12.7	19.9	1.8	5.4	0	1.3
	28	22	≤10	9	—	≤10
S14	6.7	6.8	5.6	37.8	0	9.0
	28	22	17	11	—	≤10

Table 3. Cod egg abundances and ages from stations across Trinity Bay and from near an aggregation of cod spawning over Heart's Ease Ledge, Trinity Bay, 3–7 July 1993 (the egg ages are for the oldest eggs in the sample).

Station	Egg abundance (eggs·1000 m^{-3})	Age (d)
Heart's Ease Ledge 1 (3 July)	61.1	≤10
Heart's Ease Ledge 2 (3 July)	69.2	≤10
Heart's Ease Ledge (6 July)	9.5	≤10
Trinity Bay 1 (2 July)	29.6	≤10
Trinity Bay 2 (2 July)	0.6	≤10
Trinity Bay 3 (2 July)	0.4	≤10
Trinity Bay 4 (2 July)	1.0	≤10

The proportion of ripe/spawning (stage 2) and spent/partially spent (stage 3) individuals (total 53 fish) differed over the 4 d of sampling between 2 and 7 July (Fig. 5). This difference was significant when tested using the log likelihood ratio test with William's correction (Sokal and Rohlf 1981) (G_{adj} = 6.068, p = 0.0102; n = 53, df = 1). Twenty-six fish were captured alive and transported to Memorial University's Marine Science Research Laboratory, Logy Bay. Several fish spawned in holding tanks several days later. Fertilized eggs were collected and hatched in the laboratory (Leader 1994).

Evidence for inshore spawning from ichthyoplankton surveys, 1991 and 1993

Identifiable cod and chw eggs were found on all sampling dates, except for September 1991 (Tables 2 and 3). The highest egg concentrations were sampled from Station S6 in Northwest Arm on 29 June 1993. Stations S6, S7, and S8 in Northwest Arm displayed the greatest abundance of eggs in July and August 1991 and July 1993. Overall, egg abundances ranged from 0 to 349 eggs·1000 m^{-3}. Sampling near the spawning aggregation of cod over Heart's Ease Ledge, 3–6 July 1993, netted early-stage eggs in concentrations up to 69 eggs·1000 m^{-3} (Table 3). Samples from the transect across Trinity Bay on 2 July 1993 contained the lowest numbers of eggs recorded in July of either year.

The highest concentrations of young eggs were collected on the July and August (1991 and 1993) survey dates at Stations S6, S7, and S8 in Northwest Arm and over the spawning aggregation over Heart's Ease Ledge in 1993 (Tables 2 and 3). The oldest eggs at these sites were 10–17 d old. The youngest eggs (≤10 d) in the study were found during the two months of July and August. Back-calculations place the probable date of spawning of these eggs within the window (mid-June to mid-July) estimated from spawning cod in commercial catches discussed above. The estimated birthdate of cod eggs sampled in July and August 1991 ranged between 30 June and 4 August (calendar days 181–216). The oldest eggs found near the spawning aggregation over Heart's Ease Ledge have a calculated spawning date of 18–26 June (days 169–177).

Few cod larvae and no haddock or witch flounder larvae were collected in the survey. All but one of the larvae collected in 1991 were <14.5 mm in total length. Eighty-one percent of posthatch larvae collected were ≤7.0 mm in length.

© 1997 NRC Canada

Discussion

Period of inshore spawning

Atlantic cod spawned in Trinity Bay in the early summer during each year of the study. This conclusion is based on (1) the observed progressive maturation of bay cod from spawning to spent condition, (2) direct observation of a spawning aggregation of cod over Heart's Ease Ledge, and (3) the presence of recently spawned (≤10 d) cod eggs in the study region.

The data from commercial and experimental catches in the Random Island area of Trinity Bay document the development of gonadal tissue in adult cod in the bay during the spring of three consecutive years (1991–1993). The data suggest that the peak of the spawning period occurred from mid-June through mid-July. The observation of a spawning aggregation in early July 1993 over Heart's Ease Ledge occurred within the temporal range for inshore spawning estimated from the commercial catch data in the region in 1991 and 1992. The school was found at temperatures (2–4°C) that have been hypothesized to be associated with the initiation of spawning. Estimated ages of young cod eggs collected in the region provide spawning times that are also within the spawning period delineated by the commercial catch data.

The lengths at 50% maturity calculated from the inshore commercial catch data are comparable with current estimates for Divisions 2J3KL from research vessel offshore surveys (Taggart et al. 1994). Combined 1991 and 1992 M_{50} values for Random Island females (47.5 cm) are smaller than the M_{50} value for Division 3L females (55.5 cm) and slightly less than the M_{50} value (49.3 cm) estimated for female cod throughout Division 2J3KL. Random Island males (M_{50} of 45.7 cm) are similar to Division 3L males (M_{50} = 45.3 cm), but larger than Division 2J3KL males (M_{50} of 39.3 cm). All estimated M_{50} values fall within 1 SD of each other.

The spawning period estimated in this study is consistent with other research findings. Methven and Bajdik (1994) reported that the timing of the initial appearance and settlement of pelagic juvenile cod in coastal regions of Trinity Bay is usually during the last 2 wk of August and the first 2 wk of September. These authors reported two periods of high abundance of pelagically coloured juvenile cod (August–September and October–November) at the southern end of Trinity Bay for the years 1982–1983 and 1989–1990. Calculated estimates of the time of fertilization of the August–September juveniles coincide with the June – early July peak spawning interval (days 165–195) estimated in the present study.

Anderson et al. (1993) back-calculated spawning times from lengths of larval cod found in Trinity Bay. They computed peaks in cod spawning of May 1984 (days 130–140) and late May – early June 1985 (days 140–160). The authors concluded that an offshore source for these larvae was unlikely and that these larvae probably originated from inshore spawning in the Trinity Bay area. In contrast, Anderson et al. (1993) computed an April peak in offshore spawning for the same years. Graham (1922) and Thompson (1943) reported the presence of cod in spawning condition in Trinity Bay during the summer months (days 121–181). Examining historical data, Hutchings et al. (1993) reported the presence of adult cod in spawning condition in May–June 1967 (days 121–181) at locations in Trinity Bay.

A model for the timing of inshore spawning

The peak inshore spawning period (mid-June through July) recently observed for Trinity Bay occurs later than the estimated time of peak spawning over the continental shelf. Templeman (1979) stated that the Labrador – East Newfoundland cod stock spawns from March through May, with spawning occurring later with decreasing latitude. Templeman (1979) maintained that most of the spawning offshore is completed by June, but can be delayed in years of unusually cold seawater temperatures. Cod overwintering in Trinity Bay experience lower water temperatures (below −1°C) (Wroblewski et al. 1994; Goddard et al. 1994) than cod on the continental shelf during the winter months (0–4°C) (Templeman 1979; Rose 1993). Thus, subzero temperatures in inshore waters may delay spawning in cod that spend the winter near the coast. Myers et al. (1993) reported a mean spawning time of day 160 for cod in Division 3L (shelf depths <201 m). This is considerably later than the times reported for the Northeast Newfoundland Shelf (days 97–138). The shallow area of Division 3L is cooler on average than the deeper continental shelf to the north (Petrie et al. 1992), supporting the hypothesis that cold water may delay maturation in northern cod.

To further test this hypothesis, temperature-dependent oocyte development rates estimated by Kjesbu (1994) can be used to determine if ambient temperature could explain the timing of spawning observed in the Random Island region of Trinity Bay. Kjesbu (1994) used diameter measurements of the most mature oocytes, as sampled by ovarian catheterization, to predict the initiation of spawning in female Atlantic cod from Norwegian waters. The author utilized regression analysis to estimate the parameters of a negative power function, such that

$$(1)\quad y = 3.33 \times 10^6 x^{-1.817}$$

where y = time to commencement of spawning (days) and x = most mature oocyte diameter (300 μm < x < 750 μm). These experiments were conducted at 9°C. Kjesbu (1994) then calibrated the time to initiation of spawning (y) calculated from Equation 1 to lower temperatures using the Q_{10} rule (e.g., Eckert et al. 1988):

$$(2)\quad R_2 = R_1 Q_{10}^{(T_2 - T_1)/10}$$

where R_2 = developmental rate (day^{-1}) at temperature T_2 (degrees Celsius), R_1 = developmental rate (day^{-1}) between the time of observation of the most mature oocyte diameter and the initiation of spawning at T_1 (9°C), and Q_{10} = 2.0 (after Kjesbu 1989).

Equation 2 can be used to calibrate Kjesbu's (1994) results to the much lower temperatures recorded in the Random Island area of Trinity Bay during the study period (Fig. 2). For example, one can use the monthly temperature from November 1991 to mid-June 1992 at Station S4 in Northwest Arm, Trinity Bay (Figs. 1 and 2). Assuming cod will reside in warm waters where possible (Goddard et al. 1994), monthly temperature was calculated by averaging from the surface to the depth of the 0°C isotherm. For winter temperature profiles that were totally subzero from the surface to the bottom, the temperature was averaged over the entire water column.

Model calculations (Fig. 6) demonstrate that lower ambi-

© 1997 NRC Canada

Table 4. Estimated spawning times and oocyte developmental period of Atlantic cod in Trinity Bay and over the Northeast Newfoundland Shelf in 1991 and 1992.

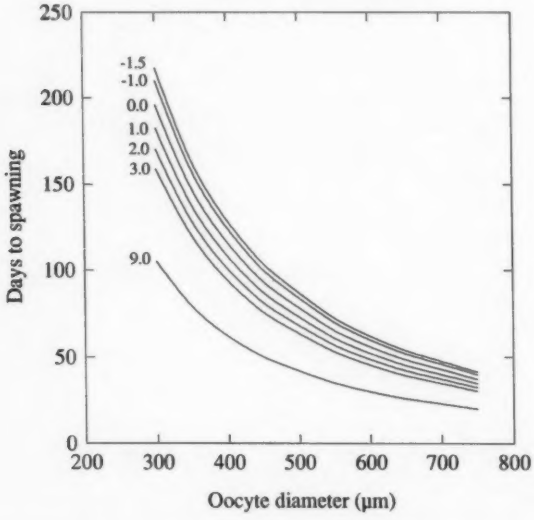
Spawning area (and data source)	Spawning window (day of year)		Average temperature (°C)		Developmental period (d)	
	1991	1992	1991	1992	1991	1992
Trinity Bay (this paper)	165–195	165–195	—	0.54	—	189
Northeast Newfoundland Shelf (Rose 1993)	≤165[a]	≤185[a]	2.5[b]	2.5[b]	165	165
Northeast Newfoundland Shelf historical average (Templeman 1979; Myers et al. 1993)	138 ± 36 (mean ± SD)		3.0[b]	3.0[b]	159	159

Note: Developmental periods are calculated following the relationship of temperature-dependent oocyte development as expressed in Equations 1 and 2 (from Kjesbu 1994).

[a]Dates of spawning for offshore shoals of Northeast Newfoundland Shelf cod in 1991 and 1992 represent the time at which 90% of the mature females in the sample are spent.

[b]Average temperatures calculated from data in the source documents.

Fig. 6. Estimated effects of water temperature (−1.5 to 9°C) on the initiation of spawning in individual female Atlantic cod in relation to the most mature oocyte diameter (after Kjesbu 1994).



ent temperatures considerably delay time of spawning. For example, at temperatures of 2–3°C, which approximates offshore overwintering thermal conditions (Templeman 1979; Rose 1993), the developmental period (days to spawning) of a 300-μm oocyte is 159–171 d. Atlantic cod initiate vitellogenesis from September to November (Kjesbu 1991). Assuming an overall average temperature from November 1991 until the middle of June 1992 in the study region of 0.54°C, the spawning developmental period for inshore cod is 189 d (Table 4). This amounts to an estimated delay of 18–30 d when compared with the computed commencement of spawning on offshore grounds with water temperatures of 2–3°C.

Kjesbu's (1994) equations of temperature-dependent oocyte development provide estimates of spawning times that fit the 1991–1993 observations. The model predicts a delay in the beginning of the spawning period in Trinity Bay of at least 30 d compared with historical offshore spawning times of Atlantic cod provided by Templeman (1979) and Myers et al. (1993). In 1991, adult cod from the Random Island region had begun their main spawning period when offshore spawning in NAFO Division 3L (observed by Rose 1993) was nearly complete (a difference in spawning seasons of approximately 1 mo). Model predictions of a delay in spawning by cod of 30 d are in phase with observed spawning delays of at least 30 d in 1991 and an absolute minimum of 10 d in 1992.

Evidence for delayed spawning arising from unusually cold seawater temperatures has been reported by others. Hutchings and Myers (1994) concluded that interannual variation in the spawning time of cod in NAFO Division 3L was significantly associated with variation in water temperature prior to spawning. In Division 3Ps, above-normal temperature was associated with earlier spawning.

Brander (1994) found no association between mean seawater temperature and mean date of spawning of cod around the British Isles. However, these Atlantic cod are not exposed to ocean temperatures below 0°C.

Other factors affecting inshore spawning times

Estimation of spawning times for bay cod may be confounded by fish that move to the coast from offshore overwintering grounds and then spawn in the bay. Present technology cannot differentiate between these components. Antifreeze glycoproteins were not detected in the plasma of fish sampled from the spawning aggregation over Heart's Ease Ledge (S. Goddard, Marine Science Research Laboratory, Memorial University of Newfoundland, St. John's, NF A1C 5S7, unpublished data). Tissue samples from the aggregation did not show a significant differentiation in mtDNA from offshore cod, nor from cod overwintering in the Random Island region (Carr et al. 1994). An inshore migratory component of the spawning population may experience warmer temperatures than cod overwintering in Trinity Bay, affecting their gonadal development rates and increasing the variance in the inshore spawning period. The thermal history of individual

© 1997 NRC Canada

Atlantic cod overwintering in Trinity Bay will affect the fit of the oocyte development model to observed spawning times. Active temperature selection by some cod for waters >0°C would lead to a range of oocyte developmental rates (see Goddard et al. 1994; Wroblewski et al. 1995).

There may also be a spawning temperature threshold, whereby adult cod ripen over the oceanographic winter, but delay spawning until a minimum ambient temperature is experienced (e.g., 0°C) in the spring. Studies involving other fish species found instances where the spawning cycle was delayed in individual fish that reached spawning condition. The retention of maturity stage has been reported in female Atlantic herring (*Clupea harengus*) (Ware and Tanasichuk 1990) and in female capelin (*Mallotus villosus*) (Forberg 1983). Wasserman and Smith (1978) state that full-grown oocytes can remain in a condition of physiological immaturity for extended periods of time, until they resume meiosis in response to an appropriate stimulus.

There is strong evidence to suggest that the temporal distribution of spawning by bay cod is influenced by temperature. The timing of the inshore spawning window is in phase with predictions by the oocyte development model. The hypothesis that inshore cod spawning sites are related to oceanographic temperature and bathymetric features could not be fully addressed due to the discovery of only one spawning aggregation, and requires further investigation. Our documentation of recent inshore spawning times may prove useful in managing the recovery of the northern cod stock (Lear and Parsons 1993). One option would be the closure of inshore spawning areas during the peak spawning period (e.g., June–July). Further study of inshore spawning cod is important in light of the present low spawning biomass estimates for northern cod.

Acknowledgements

We would like to thank G. Rose and D. Schneider for comments on a previous version of the manuscript and two anonymous reviewers for their insight. W. Bailey, B. Dean, M. Hickey, C. Seward, and the crews of the C.F.V. *Northern Quest* and the C.R.V. *Shamook* provided valuable assistance during the field studies. R.K.S. was supported by a Graduate Studies Fellowship from Memorial University. This study was funded by the Natural Sciences and Engineering Research Council of Canada (NSERC), National Sea Products Ltd., and Fishery Products International Ltd. under NSERC's Research Partnerships Program.

References

Anderson, J.T., Dalley, E.J., and Carscadden, J.E. 1993. Distribution and abundance of pelagic 0-group cod in inshore and offshore areas for the northern cod stock (NAFO 2J3KL). NAFO SCR Doc. 93/30, Ser. No. N2210.

Bowering, W.R., Power, D., and Brodie, W.B. 1993. The status of the witch flounder stock in Division 2J, 3K, and 3L. DFO Atl. Fish. Res. Doc. 93/49.

Brander, K.M. 1994. The location and timing of cod spawning around the British Isles. ICES J. Mar. Sci. **51**: 71–89.

Carr, S.M., and Marshall, H.D. 1991. Detection of intraspecific DNA sequence variation in the mitochondral cytochrome *b* gene of Atlantic cod (*Gadus morhua*) by the polymerase chain reaction. Can. J. Fish. Aquat. Sci. **48**: 48–52.

Carr, S.M., Snellen, A.J., Howse, K.A., and Wroblewski, J.S. 1994. Mitochondrial DNA sequence variation and genetic stock structure of Atlantic cod (*Gadus morhua*) from bay and offshore locations on the Newfoundland continental shelf. Mol. Ecol. **4**: 79–88.

Eckert, R., Randall, D., and Augustine, G. 1988. Animal physiology: mechanisms and adaptations. W.H. Freeman and Company, New York.

Fahay, M.P. 1983. Guide to the early stages of marine fishes occurring in the western North Atlantic Ocean, Cape Hatteras to the southern Scotian Shelf. J. Northwest Atl. Fish. Sci. **4**: 1–423.

Fitzpatrick, C., and Miller, R.J. 1979. Review of spawning times and locations for some commercial finfish on the Newfoundland and Labrador coasts. Fish. Mar. Serv. Tech. Rep. 905.

Forberg, K.G. 1983. Maturity classification and growth of capelin, *Mallotus villosus* (M), oocytes. J. Fish Biol. **22**: 485–496.

Goddard, S.V., Kao, M.H., and Fletcher, G.L. 1992. Antifreeze production, freeze resistance, and overwintering of juvenile northern cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **49**: 516–522.

Goddard, S.V., Wroblewski, J.S., Taggart, C.T., Howse, K.A., Bailey, W.L., Kao, M.H., and Fletcher, G.L. 1994. Overwintering behaviour of adult Northern cod (*Gadus morhua*) in cold inshore waters as evidenced by plasma antifreeze protein levels. Can. J. Fish. Aquat. Sci. **51**: 2834–2842.

Godø, O.R., and Sunnanå, K. 1984. Spawning area and distribution of 0-group cod, *Gadus morhua* L., on the Møre coast. *In* The propagation of cod *Gadus morhua* L. *Edited by* E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Flodevigen Rapp. **1**: 519–532.

Graham, M. 1922. Investigations comprising observations on the natural history of the Newfoundland shore cod. Report to the Director of Fishery Investigations, Fisheries Laboratory, Lowestoft, U.K.

Hutchings, J.A., and Myers, R.A. 1994. Timing of cod reproduction: interannual variability and the influence of temperature. Mar. Ecol. Prog. Ser. **108**: 21–31.

Hutchings, J.A., Myers, R.A., and Lilly, G.R. 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2457–2467.

Jakobsen, T. 1987. Coastal cod in northern Norway. Fish. Res. **5**: 223–234.

Kjesbu, O.S. 1989. The spawning activity of cod, *Gadus morhua* L. J. Fish Biol. **34**: 195–206.

Kjesbu, O.S. 1991. A simple method for determining the maturity stages of Northeast Arctic cod (*Gadus morhua* L.) by *in vitro* examination of oocytes. Sarsia, **75**: 335–338.

Kjesbu, O.S. 1994. Time of start of spawning in Atlantic cod (*Gadus morhua*) females in relation to vitellogenic oocyte diameter, temperature, fish length and condition. J. Fish Biol. **45**: 719–735.

Kjesbu, O.S., Whitthames, P.R., Solemdal, P., and Greer Walker, M. 1990. Ovulatory rhythm and a method to determine the stage of spawning in Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **47**: 1185–1193.

Leader, L. 1994. To feed or not to feed?: Ontogeny of foraging and predator advoidance trade-offs in larval cod (*Gadus morhua*). M.Sc. thesis, Memorial University of Newfoundland, St. John's, Nfld.

Lear, W.H. 1984. Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, as inferred from tagging studies. J. Northwest Atl. Fish. Sci. **5**: 143–159.

Lear, W.H., and Parsons, L.S. 1993. History and management of the fishery for northern cod in NAFO Divisions 2J, 3K and 3L. *In* Perspectives on Canadian marine fisheries management. *Edited by* L.S. Parsons and W.H. Lear. Can. Bull. Fish. Aquat. Sci. **226**: 55–90.

McKenzie, R.A. 1940. Nova Scotian autumn cod spawning. J. Fish. Res. Board Can. **5**: 105–120.

© 1997 NRC Canada

Methven, D.A., and Bajdik, C. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 78–90.

Morrison, C.M. 1990. Histology of the Atlantic cod, *Gadus morhua*: an atlas. Part three. Reproductive tract. Can. Spec. Publ. Fish. Aquat. Sci. 110.

Myers, R.A., Mertz, G., and Bishop, C.A. 1993. Cod spawning in relation to physical and biological cycles of the northern Northwest Atlantic. Fish. Oceanogr. **2**: 154–165.

Neilsen, A. 1894. Operations at Dildo Island Hatchery. *In* Annual Report of the Newfoundland Department of Fisheries, for the year 1893. J.W. Withers, St. John's, Nfld. pp. 20–35.

Neilsen, A. 1895. Operations at the Dildo Island Marine Hatchery. *In* Annual Report of the Newfoundland Department of Fisheries, for the year 1894. J.W. Withers, St. John's, Nfld. pp. 26–48.

Page, F.H., and Frank, K.T. 1989. Spawning time and egg stage duration in northwest Atlantic haddock (*Melanogrammus aeglefinus*) stocks with emphasis on Georges and Browns Bank. Can. J. Fish. Aquat. Sci. **46**(Suppl. 1): 68–81.

Petrie, B., Loder, J.W., Lazier, J., and Akenhead, S.A. 1992. Temperature and salinity variability on the eastern Newfoundland Shelf: the residual field. Atmos.-Ocean, **29**: 14–36.

Rose, G.A. 1993. Cod spawning on a migration highway in the northwest Atlantic. Nature (Lond.), **366**: 458–461.

SAS Institute, Inc. 1989. SAS/STAT users guide, release 6.03 edition. SAS Institute, Inc., Cary, N.C.

Serebryakov, V.P. 1967. Cod reproduction in the Northwest Atlantic. Tr. PINRO, **20**: 205–242. (Fish. Res. Board Can. Transl. 1133).

Smedbol, R.K. 1994. Evidence for inshore spawning of Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, from 1991 to 1993. M.Sc. thesis, Memorial University of Newfoundland, St. John's, Nfld.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. W.H. Freeman and Company, New York.

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

Templeman, W. 1974. Migration and intermingling of Atlantic cod, *Gadus morhua*, stocks of the Newfoundland area. J. Fish. Res. Board Can. **31**: 1073–1092.

Templeman, W. 1979. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962–66. ICNAF Res. Bull. **14**: 6–50.

Templeman, W., and May, A.W. 1965. Research vessel catches of cod in the Hamilton Inlet Bank area in relation to depth and temperature. ICNAF Spec. Publ. **6**: 149–165.

Thompson, H. 1943. A biological and economic study of cod (*Gadus callarius* L.) in the Newfoundland area. Nfld. Dep. Nat. Resour. Res. Bull. No. 14.

Trout, G.C. 1957. The Bear Island cod: migration and movements. Fish. Invest. Lond. (2), **21**(6): 1–51.

Villagarcia, M.G. 1995. Structure and distribution of demersal fish assemblages on the northeast Newfoundland/Labrador Shelf. M.Sc. thesis, Department of Biology, Memorial University of Newfoundland, St. John's, Nfld.

Ware, D.M., and Tanasichuk, R.W. 1990. Biological basis of maturation and spawning waves in Pacific herring (*Clupea harrengus pallasi*). Can. J. Fish. Aquat. Sci. **47**: 2375–2379.

Wasserman, W.J., and Smith, L.D. 1978. Oocyte maturation in nonmammalian vertebrates, *In* The vertebrate ovary. *Edited by* R.E. Jones. Plenum Press, New York. pp. 443–468.

Wroblewski, J.S., Collier, A., and Bailey, W. 1993. Ocean temperatures in the Random Island region of Trinity Bay, 1991–1992. The NSERC/ Fishery Products International/ National Sea Products Chair in Fisheries Oceanography, Data Report No. 1. Memorial University, St. John's, Nfld.

Wroblewski, J.S., Bailey, W.L. and Howse, K.A. 1994. Overwintering of adult Atlantic cod (*Gadus morhua*) in nearshore waters of Trinity Bay, Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 142–150.

Wroblewski, J.S., Goddard, S.V., Smedbol, R.K., and Bailey, W.L. 1995. Movements of Atlantic cod (*Gadus morhua*) within the spring thermocline in Trinity Bay, Newfoundland. J. Mar. Biol. Assoc. U.K. **75**: 265–284.

© 1997 NRC Canada

Geographic contraction in juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances

David C. Schneider, David A. Methven, and Edgar L. Dalley

Abstract: There is now evidence for both pelagic and demersal fish species that reduction in density at the spatial scale of an entire stock does not necessarily reduce local density or catch rate. This works against conservation of exploited populations by preventing those engaged in fishing from sensing stock declines. Decoupling of local change in density from larger scale changes can result from range contraction at low stock size. MacCall's theory of range contraction due to optimal habitat selection led us to test whether contraction occurs during demersal juvenile stages of Atlantic cod (*Gadus morhua*) for which contraction has been confirmed in mature stages at low stock sizes. Contraction was analyzed from catches of small cod in three length groups corresponding to ages 0+, 1+, and 2+ using data from 1959–1964 and 1992–1994 at a series of coastal sites extending over 1500 km of coastline. In years of low cohort size, contraction did not occur relative to geographically fixed foci or annually shifting foci in any of the three length groups. Absence of range contraction means that year-to-year change in the size of newly settled cohorts of cod, at the scale of the coastline, can be estimated from change in local density.

Résumé : Nous disposons à présent d'indications selon lesquelles, chez les poissons pélagiques comme chez les poissons de fond, la réduction de la densité à l'échelle d'un stock entier n'entraîne pas nécessairement une réduction de la densité locale ni des taux de capture. Cela nuit aux efforts de conservation des populations exploitées dans la mesure où ceux qui travaillent dans le domaine de la pêche ne peuvent pressentir le déclin des stocks. La dissociation observée entre les changements dans la densité locale et ceux qui surviennent sur une plus grande échelle peut découler d'une contraction du territoire occupé par le stock lorsque celui-ci est de taille réduite. La théorie avancée par MacCall selon laquelle la contraction du territoire résulte de la sélection de l'habitat optimal nous a amenés à examiner l'éventualité d'une contraction au cours des stades juvéniles démersaux chez la morue franche (*Gadus morhua*), espèce pour laquelle il a été confirmé qu'une contraction survient aux stades adultes, lorsque les stocks sont réduits. Nous avons analysé la contraction à partir de données sur les prises relatives à de jeunes morues de trois catégories de taille correspondant aux âges 0+, 1+ et 2+, données recueillies au cours des années 1959 à 1964 et 1992 à 1994, à une série de sites côtiers s'étendant sur plus de 1 500 km le long de la côte. Dans les années où la taille des cohortes était réduite, aucune contraction n'a été observée, dans aucune des trois catégories de taille, par rapport à des foyers géographiques fixes ni par rapport à des foyers changeant d'une année à l'autre. L'absence de contraction du territoire occupé signifie que, d'année en année, les changements dans l'importance des cohortes de morues nouvellement établies peuvent être estimés, à l'échelle de la côte, à partir des changements dans la densité locale.
[Traduit par la Rédaction]

Introduction

The assumption of constant catchability is now known to be suspect in any fishery, whether pelagic or demersal. Catchability increases as stock size decreases in pelagic species (reviewed by Winters and Wheeler 1985) and in semidemersal species: Cape hake (*Merluccius capensis*) (Gordoa and Hightower 1991) and whiting (*Merlangius merlangus*) (Cook and Armstrong 1985). Catchability also increases with decreasing stock size in demersal species: Atlantic cod (*Gadus morhua*) (Pope and Garrod 1975; Houghton and Flatman 1982; Cook and Armstrong 1985; Rose and Leggett 1991) and haddock (*Melanogrammus aeglefinus*) (Crecco and Overholtz 1990). This inverse relation, which hides stock declines from those engaged in fishing, can result from any of several mechanisms. Redistribution and focusing of fleet effort is one such mechanism for which there is theoretical (Paloheimo and Dickie 1964; Clark and Mangel 1979) and empirical (Cook and Armstrong 1985) support. Decoupling of local from larger scale density due to range contraction during periods of decline (Murphy 1977) is another mechanism for which there is again theoretical (MacCall 1990) and empirical (Winters and Wheeler 1985) support.

Contraction of geographic range during stock decline is evident in distributional maps of Pacific sardine (*Sardinops sagax*) Japanese sardine (*Sardinops melanosticta*) and Peruvian anchovy (*Engraulis ringens*) (MacCall 1990). It is also evident in distributional maps for demersal species such as cod east of Newfoundland (Taggart et al. 1994). This relation between area occupied and abundance has been quantified (as

Received February 21, 1995. Accepted March 20, 1996.
J13442

D.C. Schneider and D.A. Methven. Ocean Sciences Centre, Memorial University of Newfoundland, St. John's NF A1B 3X7, Canada.
E.L. Dalley. Department of Fisheries and Oceans, Science Branch, Northwest Atlantic Fisheries Centre, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

© 1997 NRC Canada

a correlation) in a variety of pelagic species: California sardine (MacCall 1976; Radovich 1979), northern anchovy (*Engraulis mordax*) (Radovich 1976), Peruvian anchovy (Csirke 1980), Atlantic menhaden (*Brevoortia tyrannus*) (Shaaf 1980), Atlantic herring (*Clupea harengus*) (Winters and Wheeler 1985), capelin (*Mallotus villosus*) (Nakashima 1988), and longfin squid (*Loligo pealei*) (Lange 1991). Exceptions have yet to be reported for pelagic schooling species. In groundfish, positive correlation between some measure of abundance and area occupied has been reported in cod (Rose and Leggett 1991; Swain and Wade 1993; Swain and Sinclair 1994) and haddock (Crecco and Overholtz 1990; Marshall and Frank 1994). Exceptions occur when measures of mean distance from centres of distribution (Murawski and Finn 1988) are used (Marshall and Frank 1994).

Geographic contraction has also been evaluated with quantile plots, which provide more information than a single statistic such as a correlation coefficient. Quantile plots showing cumulative percent numbers or biomass relative to cumulative percent area become increasingly concave as animals become more concentrated. As judged from quantile plots, Cape hake became increasingly concentrated during two successive years of decline in stock size (Gordoa and Hightower 1991). Further concentration did not occur during two years of continued decline. Quantile plots and an index based on these plots (Myers and Cadigan 1995) indicated that in the area east of Newfoundland, cod became increasingly concentrated from 1984 through 1992. The spawning stock biomass was estimated to have held steady from 1984 to 1988 and then decline rapidly (Bishop et al. 1993).

Theory and observation indicate that body size (which in turn depends on age) modifies the relation between geographic contraction and decrease in population size. Mobility, which depends on body size, can in theory limit the rate of contraction. Competition and predator avoidance, which also depend on body size, can theoretically affect rate of geographic contraction (MacCall 1990; Swain 1993). Figure 5 in Swain and Wade (1993) shows more dramatic reduction in range in older cod than in age 3 cod during years of low stock size. Figure 8 in Swain and Sinclair (1994) shows that the area over which 50% of cod were found expanded significantly with population size in young (age 3) but not older cod. Marshall and Frank (1994) found that mean distance from the centre of distribution was positively associated with overall abundance in juvenile haddock, but not in larger (older) haddock.

Any of several different behaviours can cause geographic contraction during population decrease. The list includes predator avoidance by schooling behaviour (Radovich 1979; Clark and Mangel 1979), swamping of egg predators by attraction to spawning aggregations, greater migratory range in large stocks composed of large fish (Winters and Wheeler 1985), and density-dependent habitat selection (MacCall 1990). The last can, in theory, be important in demersal species during the period immediately after settlement to the seafloor. Pelagic stages of many demersal species travel substantial distances before settlement and then show greater selectivity for shallow-water habitats than older stages (Sinclair 1992; Macpherson and Duarte 1991). Postsettlement stages of cod on Georges Bank are confined to restricted areas, compared with earlier or later stages (Lough et al. 1989; Wigley and Serchuk 1992). Juvenile stages of cod are associated with coarse substrate (Lough et al. 1989), often with macrophytic algae or seagrass, in both the eastern (Tveite 1984) and western Atlantic (Keats et al. 1987). This pattern of definable habitat by depth and substrate, together with increasing mobility as fish approximately double in length during the first and again in the second year of life, sets the stage for density-dependent habitat selection, resulting in measurable geographic contraction during years with low numbers. Olsen and Soldal (1989) hypothesized that suitable coastal habitats are fully utilized by juvenile cod, regardless of cohort size. They provided no evidence for density-dependent habitat selection, nor did they show that it results in geographic contraction and decoupling of local density from cohort size.

To test for geographic contraction during the early demersal stage, we compared the distribution of cod in three years of low cohort strength (after the collapse of the fishery in 1992) with distribution across the same series of locations from 1959 through 1964. Geographic contraction was evaluated graphically within a fixed coordinate framework by mapping counts on the same grid and then examining the map for patterns of contraction into restricted parts of the grid during years of low overall abundance. To test for contraction, sites were ranked within the year with the best spatial coverage (1962); this arrangement of sites was then used to evaluate whether geographic contraction, as judged from more concave plots of density across sites, occurred in lower ranking years. Geographic contraction was also quantified relative to shifting foci of aggregation. Sites were reranked each year to produce smooth plots, which were then compared to test for an increasingly concave profile in years of low abundance. These plots have the same shape as quantile–quantile plots, except that they are not expressed as cumulative percentages.

Geographic contraction, like many ecological phenomena, may be more evident at some scales of spatial resolution than others. We evaluated geographic contraction at the scale of bays along the Newfoundland coast, as well as at the scale of individual sites (each approximately 16 m × 55 m = 880 m^2) along the coast. Because of the limited mobility of juvenile cod (Tupper and Boutelier 1995), we expected greater contraction at the scale of sites than at the scale of bays.

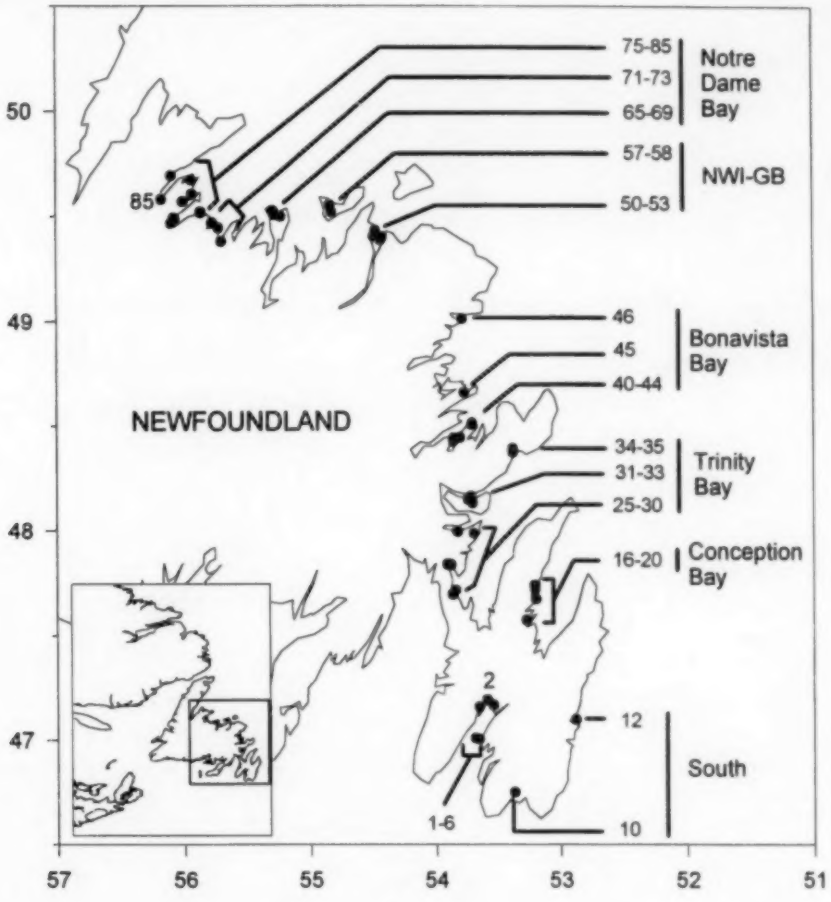
Methods

Counts of juvenile cod were made by hauling a bottom seine toward the beach at a series of sites along the eastern coast of Newfoundland, from St. Mary's Bay northward to Bonavista Bay and westward through Notre Dame Bay (Fig. 1). Each site in Fig. 1 is listed by name in the Appendix (Table A1), with latitude and longitude. Counts were made at the same time each year, from mid-September to late October. Sites were visited in the same sequence each year, so that each bay or section of coast was sampled within a week or two of the same calendar date (Appendix, Table A2).

During 1959–1964, sites were visited from a small research vessel that moved along the coast. Fish were collected with a 25-m bottom seine deployed from a small boat. Net specifications are described in Lear et al. (1980). From 1992 onward, sites were visited with a motorized boat. Deployment began with one person standing on the beach holding one of the hauling ropes. The rope and then the seine were fed from the boat as it backed away from the beach to a distance of 55 m. Once the net was in the water the boat headed back to shore, paying out the second hauling line. When the boat reached the shore a second person then jumped from the boat with the second

© 1997 NRC Canada

Fig. 1. Distribution of 56 sampling sites (numbers) along the eastern coast of Newfoundland. NW1-GB, New World Island and Gander Bay.



hauling line. Once the net had sunk to the bottom, it was hauled in. Hauling on the two lines was coordinated to an equal rate by calling out the arrival of knots placed at 10-m intervals on each line. The two hauling points remained separated until the seine approached the shore, when the hauling ropes were drawn closer together to reduce spread in the wings of the seine and prevent escapement. The net fished from the bottom to about 2 m off the bottom, at an average maximum depth of 4–6 m in all years.

For the 1992 survey, a bottom seine was purchased and then modified so that dimensions and method of deployment were as similar as possible to the 1959–1964 surveys. The modified seine had a headrope length of 24.4 m and a footrope of 26.2 m. The wings, belly, and codend were constructed of knotless nylon netting, 19-mm stretch mesh in the wings and belly and 12.7-mm stretch mesh in the codend. The codend was lined with a knotless nylon netting of 9-mm stretch mesh. Cotton netting, used in the earlier survey, could not be obtained. The Dan Leno Sticks on each wing of the seine where the two hauling ropes are attached were 75 cm long and 25 mm in diameter and made of aluminum. The net had a weighted footrope to hold it in contact with the bottom, and floats at the headline to hold it upright. Mr. Tom Collier (Department of Fisheries and Oceans), who participated in the 1959–1964 surveys, made a trip into the field in 1992 to compare execution with the earlier survey. After viewing the sampling procedure, he suggested several changes to arrive at a protocol as similar as possible to that used in the 1960s. One such change was that the seine was paid out from the boat, rather than from the beach. The most notable change was the distance between the two hauling points on the beach. This was adjusted on the beach until it matched Mr. Collier's recollection and then measured. This distance (16 m) was almost exactly half that (100 ft) mentioned in some of the field notes from the 1960s. We were unable to see how a 25-m seine could be fished from two beach points separated by 100 ft, so we used 16 m for all sets.

During 1992 the sites were relocated using black and white photographs of each site taken in 1962. Present-day shoreline features, underwater algae, and substrate were found to be similar to 1959–1964 as determined by photographs and station records taken during the earlier survey. Colour photographs taken in 1992 were used to relocate sites in 1993, for which the survey party differed from 1992. During the 1994 survey, a member of the 1992 party compared notes with a member of the 1993 party; relocation of sites in 1993 and 1994 was to within an average of 8 m of that in 1992, using only photographs to relocate sites.

Two or more sets were conducted at each site starting in 1960. Two consecutive sets were usually conducted when the site was initially sampled and one or more additional sets were conducted later (usually the same day, but sometimes on the next day) such that a different tidal level was sampled. The initial sets at a site were not

© 1997 NRC Canada

Table 1. Comparison of catches with and without motor, Little Mosquito Cove in 1992, in LG0 and LG1 + LG2.

Comparison	Set	Date	Motor on/off	Number of cod caught	
				LG0	LG1 + LG2
1	1	21 Oct. 1992	Off	652	5
1	2	21 Oct. 1992	On	879	6
2	1	22 Oct. 1992	Off	880	38
2	2	22 Oct. 1992	On	1964	27
3	1	28 Oct. 1992	Off	14	0
3	2	28 Oct. 1992	On	412	1

Table 2. Mean count per haul, number of sites above the median count, and sites with 95% of catch for LG0, LG1, and LG2 cod from the Fleming sites.

Year	N_{haul}	Mean count per haul			N_{sites}	$N_{>median}$			$N_{95\%}$		
		LG0	LG1	LG2		LG0	LG1	LG2	LG0	LG1	LG2
1959	12	178	5.17	1.50	6	3	3	2	2	6	2
1960	34	31.4	134	0.588	17	8	17	4	5	13	3
1961	60	11.0	27.7	2.07	30	14	20	16	12	14	12
1962	80	29.5	6.96	0.813	40	26	18	16	17	22	13
1963	82	17.8	30.7	0.439	41	26	27	11	22	13	9
1964	64	9.53	50.8	2.06	32	11	28	16	9	18	12
1992	92	9.60	3.95	0.391	46	20	4	9	18	8	8
1993	88	13.0	10.22	0.233	45	23	10	11	19	8	10
1994	80	19.8	16.45	0.937	40	15	20	20	12	18	17

Note: N_{haul} = number of hauls (two sites with only one haul per site in 1993), N_{sites} = number of sites, $N_{>median}$ = number of sites above the overall median count, within a length group, and $N_{95\%}$ = minimum number of sites accounting for 95% of fish caught in any one year, within a length group.

confined to any particular tide level or time of day, but all sets were conducted during daylight. In 1992–1994, three hauls were made at each site. Two consecutive sets were made at exactly the same location with the third set being made adjacent to the first two sets. In all nine years, the second set was usually conducted within 1 h of the first. To obtain a comparable unit of effort across all years, we used the first two hauls at each site, reported as the average catch per haul. Two sites with only a single haul were included in the 1993 data.

In 1992, several sites were found to be obstructed by fishing plants and wharfs built after 1964. These sites were dropped from the list and never revisited. During 1992, escapement from the net during hauling was checked and found to be negligible, based on direct observation by a diver swimming behind or above the net as it was hauled toward shore. From 1992 onward, sites were visited by hauling a small boat on a trailer to a convenient launching point and then motoring to the site. The boat was rowed during the earlier years, so it was thus of interest to measure whether catches from a motorized boat differed from those of a boat that was rowed during net deployment. To estimate the difference the seine was set twice, first by rowing the boat and then immediately making another haul at the same location with the motor. The comparison was made on three different dates at Fleming site No. 27 (Fig. 1; Appendix, Table A1) during October 1992.

All cod caught in the seine were measured to the nearest half centimetre (1959–1964) and nearest millimetre (1992–1994) at the end of each day. Individuals were assigned to the following length groups: LG0 (standard length (SL) < 97 mm) corresponding to age 0+, LG1 (SL = 97–192 mm) corresponding to age 1+, and LG2 (SL > 193) corresponding to age 2+.

Statistical computations were carried out with the SAS system. Assumptions for computing *p*-values from an F-distribution were checked by examining residuals for normality and for association with the structural model. A criterion of $\alpha = 5\%$ was used to declare statistical significance.

Results

The use of a motorized boat to set the seine was expected to reduce catch through noise and disturbance. Contrary to expectation, the use of the motor did not reduce catch. If anything, it increased catch of cod in length group 0 (Table 1), perhaps through greater speed in deployment of the seine. These results indicate that for LG0 cod from 1992 onward, estimates of average density of LG0 fish in the area seined are biased upward relative to the 1959–1964 data. Analyses of geographic contraction in LG0 fish were carried out twice, first with no correction and then with a correction factor (C = 2.11) calculated as the number of LGO fish caught when the motor was used (3255) divided by the number of LGO fish when the motor was not used (1546).

The average catch varied substantially from year to year (Table 2). The largest catch, 178 LG0 fish per haul in 1959,

© 1997 NRC Canada

was based on two hauls at each of six sites. Most of these fish were caught at a single site. However, this same cohort was strong the following year, when sampling was more extensive (Table 2). The 1959 cohort remained strong in 1961, when sampling was even more extensive. The estimate of cohort strength in 1959 was retained on the basis of a biological criterion, rather than rejected on exclusively statistical criteria of small sample size and large variance. The average catches of LG0 fish after stock collapse (1992–1994) were similar to the lowest catches in the early 1960s, before stock collapse. When the correction factor (C = 2.11) was applied to the 1990s data, this overlap was reduced: the highest catch in the 1990s (19.8/2.11 = 9.4 LG0 per haul) ranked below the lowest catch in the 1960s (9.5 LG0 per haul).

Geographic contraction was examined relative to both fixed and movable coordinates. The fixed coordinate analysis was carried out by arranging all sites on a single axis, distance from Fleming site No. 2, near Colinet (Appendix, Table A1). The maximum distance by water from this site (as measured with 5-km increments) was 1590 km, to King's Point (site No. 85) in western Notre Dame Bay. Degree of spatial concentration was evaluated visually by arranging graphs in order of mean annual catch, placing the year of highest mean catch at the top of the page and proceeding down the page to lowest catch at the bottom. Fig. 2 shows the results for LGO cod in nine years ranked from high to low. There was no discernable pattern of increasing concentration into a small number of sites, moving from top to bottom in Figure 2. Because of the possible upward bias on the estimates for LG0 cod, this analysis was repeated by applying the correction factor of 2.11 computed from Table 1 and then reranking the years. This dropped 1992 and 1993 to the bottom and 1994 below 1963. After reranking, there was still no obvious pattern of greater restriction to a few sites in low-ranking years. In LG1 cod (Fig. 3), there was no obvious pattern of increasing spatial concentration into fewer sites, moving down the page. Sites with high densities of LG1 cod in good years did not remain high in years with lower mean density. In LG2 cod (Fig. 4), years with a few relatively large counts (1962, 1960, 1963, 1992) tended to rank low compared with other years, suggesting some degree of increase in spatial concentration. However, the sites that accounted for a large proportion of organisms in high-ranking years did not account for a large proportion of organisms in low-ranking years.

Strong geographic contraction was not evident in this analysis, but it is possible that geographical arrangement of sites obscured a weak degree of contraction. The analysis was repeated by ranking from high to low in a year with good coverage (1962), rather than arranging sites by distance from a fixed point along the coast. This same ordering of sites on the horizontal axis was then used to compare years, with the expectation that higher ranking years would show a flatter profile, while lower ranking years would show a more concave profile than 1962 due to geographic contraction. There was no evidence for geographic contraction in LG0 cod (Fig. 5). Concavity did not increase, going from years of high abundance (top of Fig. 5) to years of low abundance (bottom of Fig. 5). This result was unchanged when years were reranked according to the correction factor computed from Table 1.

A similar lack of geographic contraction was found for LG1 and LG2 cod. The year 1962 was a relatively low-ranking year for LG1 cod. Years with lower abundances than 1962 showed a flatter rather than more concave profile (Fig. 6). Higher ranking years also showed a flatter profile, but this was not due to any pattern of reductions at sites ranking high in 1962. In 1994, for example, all of the high ranking 1962 sites had few or no fish, while a few low-ranking sites in 1962 had large numbers of fish. For LG2 cod, 1962 was an intermediate year. Years ranking lower in abundance of LG2 cod did not show more concave profiles than 1962 (Fig. 7). Higher ranking years did show a flatter profile than 1962. As with LG1 cod, this was not due to any pattern of reduction at high-density sites.

Geographic contraction was not evident when analysis was based on ranking of sites in one year only (Figs. 5–7). The result was "noisy" in the sense that low-ranking sites in one year would occasionally appear as high-ranking sites in another year. It is possible that local variation, at the spatial scale of sites, may be obscuring a larger scale pattern of geographic contraction. To test this, we grouped sites by contiguity, using bays as convenient groups (Appendix, Table A1). The 1959–1964 data were grouped together for comparison with 1992, 1993, and 1994. This analysis showed clearer spatial patterns than the analysis at the scale of sites. Historically (1959–1964) the centre of distribution for inshore LG0 cod was Trinity Bay (Fig. 8*a*). This shifted to Bonavista Bay in the 1990s. There was, however, no evidence for contraction. The spatial profile for the 1990s did not show more restricted distribution than the profile for the 1960s (Fig. 8*a*). For LG1 cod (Fig. 8*b*) the centre of distribution was Conception Bay and southward for the historical data, compared with a centre in Trinity Bay in 1994, in Conception Bay in 1993, and in Bonavista Bay in 1992. As with LG0 cod, there was no evidence of geographic contraction in the 1990s, compared with the 1960s. For LG2 cod the historical centre of distribution was Trinity Bay, compared with Bonavista Bay in the 1990s. There was no strong evidence of greater spatial concentration in the 1990s than in the 1960s.

Contraction into restricted areas may have been occurring with respect to some variable that changed position from year to year, such as perhaps location of preferred temperature. To test geographic contraction relative to shifting foci, we reranked sites within each year, from high to low. The resulting plots always show a monotonic profile, rather than the rough profile obtained when the ranking of sites in one year is used across all years. When sites were ranked within each year there was still no trend toward increasingly concave plots, going from high- to low-ranking years in LG0 cod. When years were reranked according to the correction factor of 2.11, there was no trend toward increasing concavity. The plots for LG1 and LG2 cod did show some evidence for increasing concavity in low-ranking years.

Graphical analysis produced no evidence of increasing spatial concentration, using three different forms of presentation and two different spatial scales (sites and bays). To quantify contraction, we computed the percentage of sites within each year above the median catch over all nine years, N_{median}. For LG0 cod the median was 2.5 fish per haul. Table 2 lists the number of sites above the median within each year. Percent sites ($N_{>median}/N_{sites}$) was then calculated for LG0 cod. Percent sites was not related to the mean abundance in LG0 cod

© 1997 NRC Canada

Fig. 2. Catch of cod from LG0 at sites ordered by distance from Fleming site No. 2 (see text). Years are ranked from highest mean catch (top) to lowest mean catch (bottom).

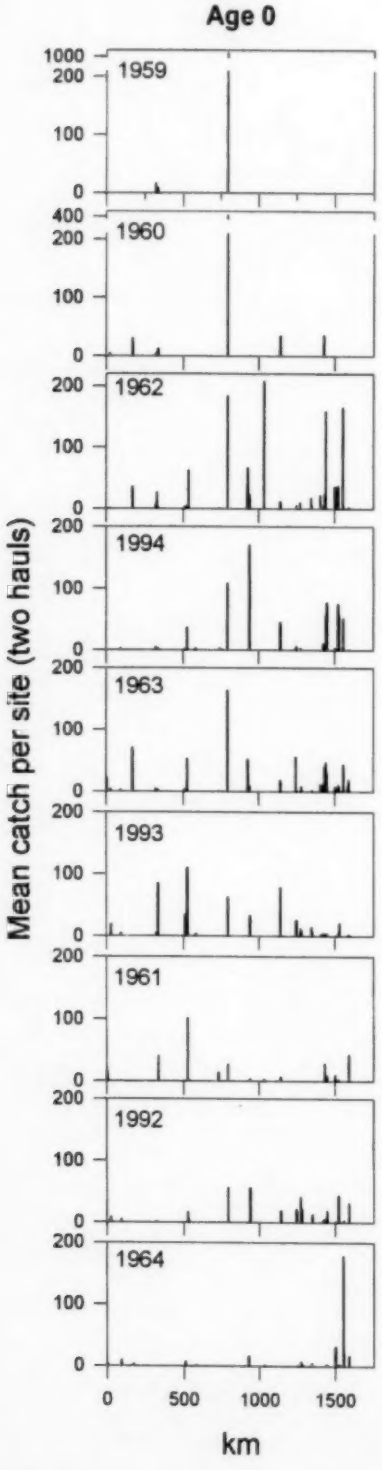
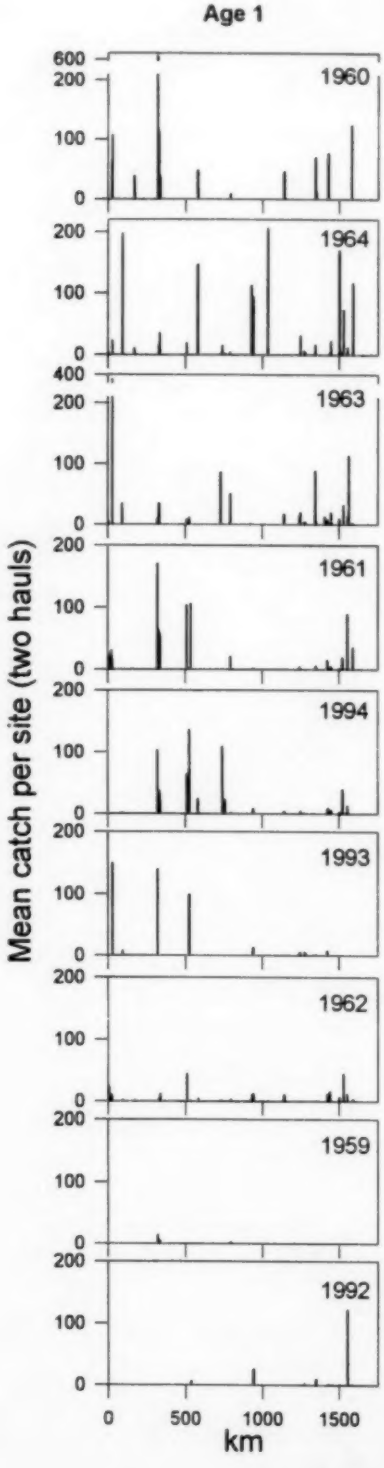


Fig. 3. Catch of cod from LG1 at sites ordered by distance from Fleming site No. 2. Years ranked from high mean catch (top) to low (bottom).



© 1997 NRC Canada

Fig. 4. Catch of cod from LG2 at sites ordered by distance from Fleming site No. 2. Years ranked from high catch (top) to low (bottom).

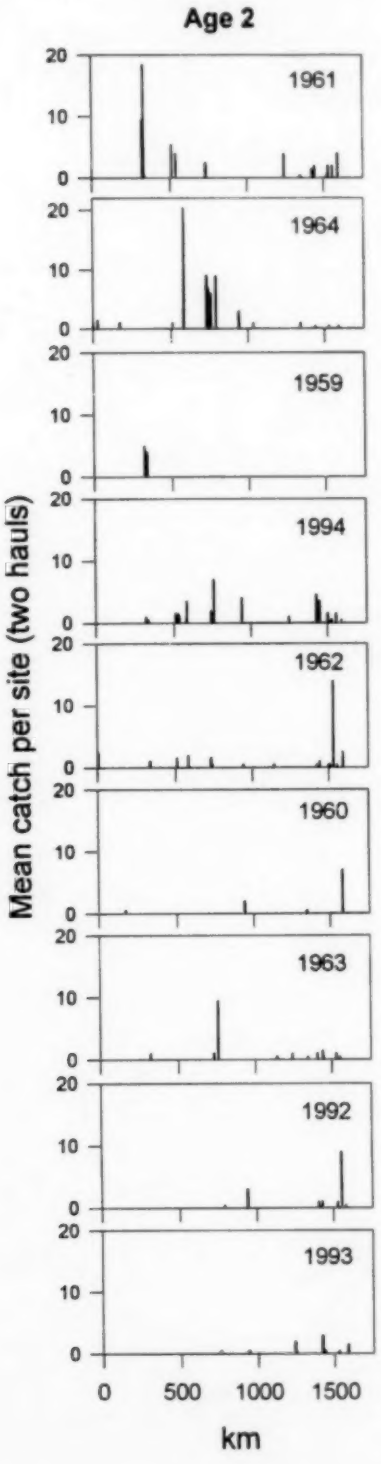
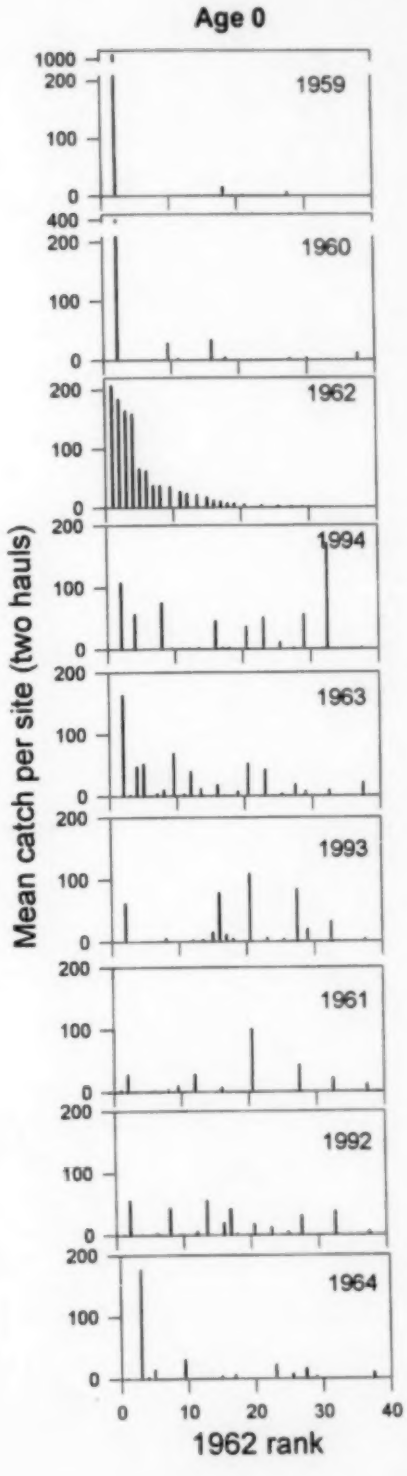


Fig. 5. Catch of cod from LG0 at sites ordered by abundance in 1962.



© 1997 NRC Canada

Fig. 6. Catch of cod from LG1 at sites ordered by abundance in 1962.

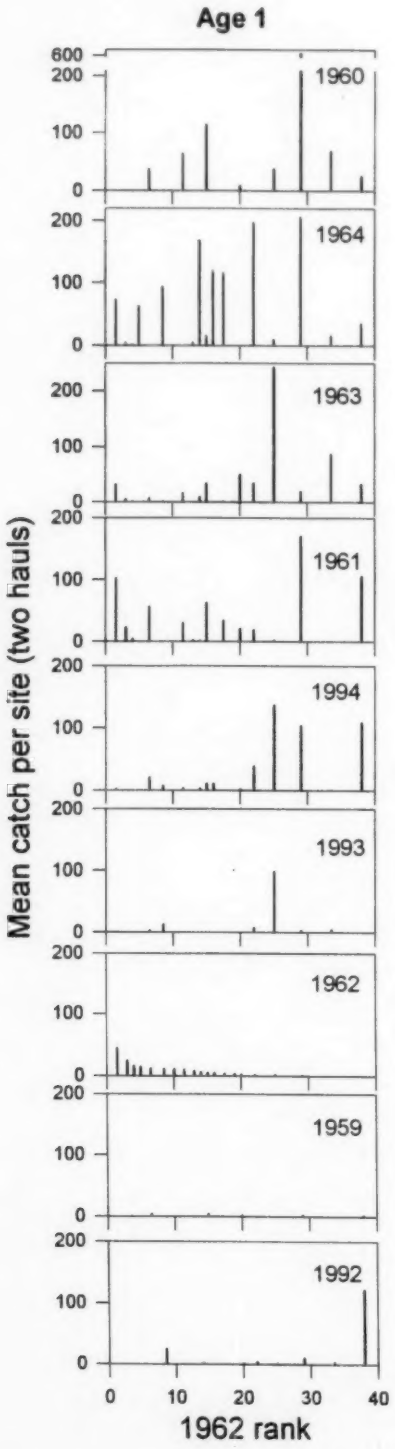
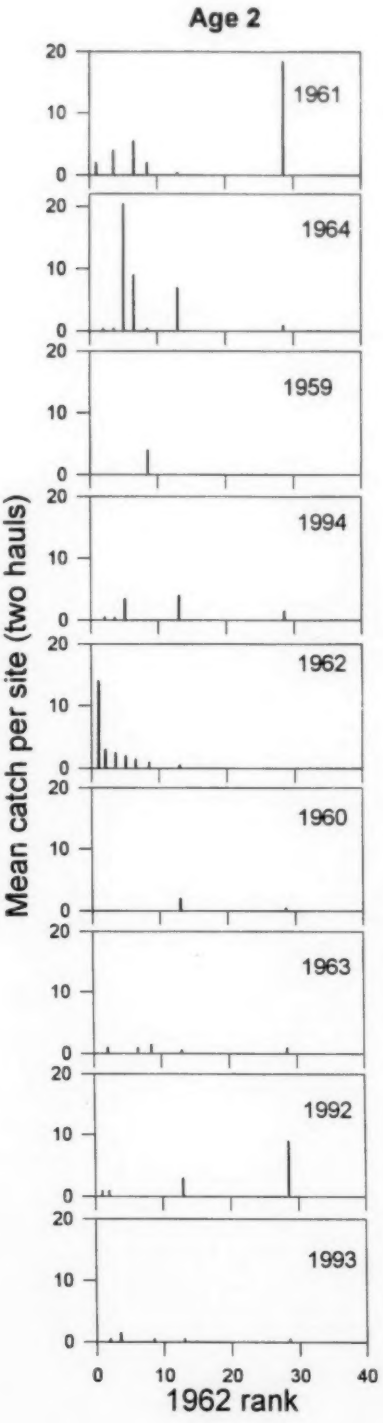
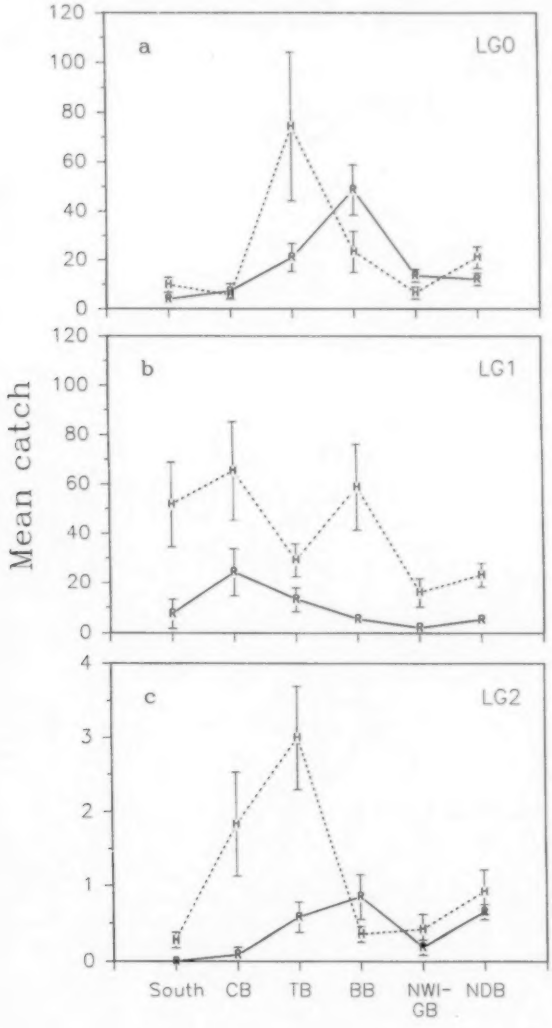


Fig. 7. Catch of cod from LG2 at sites ordered by abundance in 1962.



© 1997 NRC Canada

Fig. 8. Mean historic (H) (1959–1964) and recent (R) (1992–1994) catch of (*a*) LG0, (*b*) LG1, and (*c*) LG2 cod from sites grouped by proximity. 95% confidence limits were computed by randomization. South, St. Mary's Bay + Southern Shore; CB, Conception Bay; TB, Trinity Bay; BB, Bonavista Bay; NWI-GB, New World Island and Gander Bay; NDB, Notre Dame Bay.



($F_{1,7} = 0.09$, $p = 0.77$). The residuals for this regression were not acceptably normal, due to the influence of the 1959 datum. The relation between percent sites and abundance appeared positive when the 1959 datum was removed, but the relation was still not significant ($F_{1,6} = 1.61$, $p = 0.25$). The residuals in this analysis showed no pattern, and were normally distributed. The degree of relation remained non-significant ($F_{1,6} = 2.48$, $p = 0.17$) after applying the correction factor of 2.11 to the 1992–1994 data.

For LG1 cod the median catch was 3.5 cod per haul. The percent sites above this value increased in a linear fashion with increasing mean density in a log–log plot of the data. log(percent sites) was positively related to log(density), at a significant level ($F_{1,7} = 10.61$, $p = 0.014$). The residuals were normally distributed and hence the p-value was considered reliable.

For LG2 cod the median catch was zero. The percent sites above zero increased in linear fashion with abundance. The relation was significant ($F_{1,7} = 19.24$, $p = 0.003$). The calculation of the p-value was considered reliable, based on a check of the residuals for normal distribution.

This analysis indicates that contraction occurs in LG1 and LG2 fish, but not in LG0 fish, based on the same statistic used by Rose and Leggett (1991) to quantify geographic contraction in older (larger) cod. However, this statistic is known to increase with abundance in the absence of geographic contraction (Marshall and Frank 1994; Swain and Sinclair 1994), especially if zeros are frequent, as they were in this data set. When zeros are frequent, a better measure of geographic contraction is the minimum percentage of sites containing a substantial percentage of fish caught each year. We computed $N_{95\%}$ as the minimum number of sites containing 95% of the fish (Table 2). From this, we calculated the percentage of sites, $N_{95\%}/N_{sites}$. This percentage was not related to abundance in LG0 fish ($F_{1,7} = 0.3$, $p = 0.6$). There was no relation after correction of the 1992–1994 catches by a factor of 2.11 ($F_{1,7} = 0.5$, $p = 0.55$). In LG1 fish, this percentage of sites was not related to abundance ($F_{1,7} = 0.97$, $p = 0.36$). In LG2 cod, there was no detectable relation ($F_{1,7} = 1.32$, $p = 0.29$). The lack of association cannot be attributed to violations of assumptions for regression. Assumptions of linear relation of variables, constancy of error variance, and normal distribution of errors were checked by examining residuals for all analyses. The results of this analysis were consistent with visual impression of no contraction, and they were considered more reliable than the analysis based on percent sites above the median.

Discussion

Geographical contraction during population decline has been reported in a variety of commercially important pelagic and demersal species, including cod. From 1988 to 1994, the spawning stock of Northwest Atlantic (2J3KL) cod decreased from around 200 000 tonnes to around 2000 tonnes. These fish remained contracted into a limited area at the shelf edge, in contrast with the widespread distribution observed prior to 1988 (Taggart et al. 1994). In constrast, we found no substantial geographic contraction of LG0, LG1, or LG2 cod into limited areas along the coast. The lack of geographic contraction by LG0 cod during a period of contracted spatial distribution of adults was unexpected in light of the low population levels of juveniles, and in light of the known habitat requirements of juveniles in the first year after settlement (Lough et al. 1989; Macpherson and Duarte 1991).

This lack of geographic contraction cannot be attributed to the failure of a particular method of analysis. Visual analysis produced the same result as analysis of percent sites accounting for 95% of fish of a given size class within each year. Analysis based on percent sites above the median is known to be unreliable (Marshall and Frank 1994, Swain and Sinclair 1994) and produced results at odds with visual analysis in LG1 and LG2 fish.

© 1997 NRC Canada

We found no evidence for geographic contraction of LG0 cod, but we did find evidence that the centre of distribution for juvenile cod along the coast shifted northward in the early 1990s for LG0 and LG2 cod, compared with the early 1960s. This northward shift cannot be attributed to warmer conditions: water temperatures near the coast (Station 27) were lower in 1992 than in the early 1960s (e.g., deYoung and Rose 1993). One possible explanation for the northward shift is a reduced contribution to inshore recruitment by more southerly breeding components of cod stocks.

In our analysis of geographic contraction relative to large-scale changes in abundance from year to year, we have focused on along-shore variation within a preferred habitat in shallow water near the Newfoundland coast. Geographic contraction depicted by MacCall (1990) for pelagic species occurred primarily in a cross-shore direction, as fish became concentrated in pockets near the coast. In mature (age 5+) cod, contraction occurred into pockets along the shelf break (Taggart et al. 1994). Historical data on the cross-shore distribution of juvenile cod from Russian surveys or incidental catches were found to be too qualitatitive to examine whether LG0 fish are currently more contracted at present than in the past. It is interesting to note that postsettlement LG0 cod were confined almost entirely to coastal stations in 1992 (Dalley and Anderson 1997). Postsettlement LG0 cod were found in greater abundance in 1994 than in 1993, but maps of LG0 distribution (Dalley and Anderson 1997) show no evidence of geographic expansion away from the coast in 1994, relative to 1993.

Olsen and Soldal (1989) hypothesized that the density of demersal stages of juvenile cod would be limited in suitable coastal habitats, leading to an upper limit on density at the best sites and to expansion into poor sites in years of high abundance. We found no evidence for this in coastal habitats in Newfoundland. It is interesting to note that sites with high densities in some years can have low densities in years with high abundance, an observation that is inconsistent with density-dependent spillover during good years. The absence of spillover and geographic expansion cannot be attributed to sampling of marginal habitat. Along the east coast of Newfoundland the density of LG0 cod reaches a maximum at 4–7 m, with a relatively sharp dropoff in density at around 20 m, independent of distance from shore (D.A. Methven and D.C. Schneider, unpublished data). At the Fleming sites, the bottom seine was hauled shoreward from depths of 4–10 m, with a maximum depth of 31 m.

The observed lack of spatial contraction in LG0 fish means that density estimates from coastal waters can be used to monitor annual differences in cohort size in these same habitats. If we define cohort density $[N]$ as cohort size N per unit area A along the coast, $[N] = N A^{-1}$, then the instantaneous rate of change in cohort density is

$$\underbrace{\frac{1}{\mathrm{d}[N]}\frac{\mathrm{d}[N]}{\mathrm{d}t}}_{\text{change in density}} = \underbrace{\frac{1}{N}\frac{\mathrm{d}N}{\mathrm{d}t}}_{\text{change in cohort size}} - \underbrace{\frac{1}{A}\frac{\mathrm{d}A}{\mathrm{d}t}}_{\text{change in area}}.$$

Applying the chain rule to the change in area term:

$$\frac{1}{\mathrm{d}[N]}\frac{\mathrm{d}[N]}{\mathrm{d}t} = \frac{1}{N}\frac{\mathrm{d}N}{\mathrm{d}t} - \frac{1}{A}\frac{\mathrm{d}A}{\mathrm{d}[N]}\frac{\mathrm{d}[N]}{\mathrm{d}t}.$$

Our results show that near the coast, density does not change with area:

$$\frac{\mathrm{d}A}{\mathrm{d}[N]} = 0.$$

Hence, changes in density $[N]$ are a measure of changes in cohort size N:

$$\frac{1}{\mathrm{d}[N]}\frac{\mathrm{d}[N]}{\mathrm{d}t} = \frac{1}{N}\frac{\mathrm{d}N}{\mathrm{d}t}.$$

One of the most pressing problems in assessing commercially important species is scaling up from spatially limited estimates of density to estimates of population size at the scale of stocks. Density-based estimates of population size will be biased when aggregation error (Rastetter et al 1992) arises from a nonlinear relation between numbers and density. The results of this study indicate that the density of demersal juvenile cod is independent of area occupied within shallow (<20 m) depth ranges, and hence that an estimate of the area of suitable habitat can be used to scale up density estimates from Fleming surveys to obtain an estimate of population size of LG0 cod in shallow waters.

Acknowledgements

We thank Wade Ellis, Scott Grant, Peter Hennebury, Brian Hindy, Danny Ings, John King, and Steve Snook for help in the field. We also thank Tom Collier for help in standardizing the survey to the 1959–1964 methods. Hong Chen prepared the figures, and P.E.K. Symons and an anonymous reviewer made a number of suggestions that improved the manuscript. D.P. Swain suggested changes that substantially improved both the analysis and the manuscript. This research was funded under a 4-yr contract from the Northern Cod Science Program (Department of Fisheries and Oceans, St. John's, Nfld.).

References

Bishop, C.A., Murphy, E.F., Davis, M.B., Baird, J.W., and Rose, G.A. 1993. An assessment of the cod stock in NAFO Divisions 2J+3KL. NAFO SCR Doc 93/86, Ser. No N2271.

Clark, C.W., and Mangel, M. 1979. Aggregation and fishery dynamics: a theoretical study of schooling and the purse seine tuna fisheries. Fish. Bull. U.S. **77**: 317–337.

Cook, R.M., and Armstrong, D.W. 1985. Changes in catchability of cod, haddock, and whiting associated with the Scottish seine-net fleet. J. Cons. Int. Explor. Mer, **42**: 171–178.

Crecco, V., and Overholtz, W.J. 1990. Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. Can. J. Fish. Aquat. Sci. **47**: 385–394.

Csirke, J. 1980. Recruitment in the Peruvian anchovy and its dependence on the adult population. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **177**: 307–313.

Dalley, E.L., and Anderson, J.T. 1977. Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. **50**: 2729–2741.

Gordoa, A., and Hightower, J.E. 1991. Changes in catchability in a

© 1997 NRC Canada

bottom-trawl fishery for Cape hake (*Merluccius capensis*). Can. J. Fish. Aquat. Sci. **48**: 1887–1895.

Houghton, R.G., and Flatman, S. 1982. The exploitation pattern, density-dependent catchability, and growth of cod (*Gadus morhua*) in the west-central North Sea. J. Cons. Int. Explor. Mer, **39**: 271–287.

Keats, D.W., Steele, D.H., and South, G.R. 1987. The role of the fleshy macroalgae in the ecology of juvenile cod (*Gadus morhua* L.) in inshore waters off eastern Newfoundland. Can. J. Zool. **65**: 49–53.

Lange, A.M. 1991. Alternative survey indices for predicting availability of longfin squid to seasonal northwest Atlantic fisheries. N. Am. J. Fish. Manage. **11**: 443–450.

Lear, W.H., Fleming, A.M., and Wells, R. 1980. Results of small cod surveys in eastern Newfoundland during 1959–64. NAFO SCR Doc. 80/IX/144, No. 218.

Lough, R.G., Valentine, P.C., Potter, D.C., Auditore, P.J., Bolz, G.R., Neilson, J.R., and Perry, R.I. 1989. Ecology and distribution on juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Mar. Ecol. Prog. Ser. **56**: 1–12.

MacCall, A.D. 1976. Density-dependence of catchability coefficient in the Californian Pacific sardine, *Sardinops sagax caerula*, purse-seine fishery. Mar. Res. Comm. Calif. Coop. Oceanic Fish. Invest. Rep. **18**: 136–148.

MacCall, A.D. 1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle, Wash.

Macpherson, E., and Duarte, C.M. 1991. Bathymetric trends in demersal fish size: is there a general relationship? Mar. Ecol. Prog. Ser. **71**: 103–112.

Marshall, T., and Frank, K.T. 1994. Geographic responses of groundfish to variation in abundance: methods of detection and their interpretation. Can. J. Fish. Aquat. Sci. **51**: 808–816.

Murawski, S.A., and Finn, J.T. 1988. Biological bases for mixed species fisheries: species co-distribution in relation to environmental and abiotic variables. Can. J. Fish. Aquat. Sci. **45**: 1720–1735.

Murphy, G. 1977. Clupeoids. *In* Fish population dynamics. *Edited by* J. Gulland. John Wiley & Sons, Inc., New York. pp. 283–308.

Myers, R.A., and Cadigan, N.G. 1995. Was an increase in natural mortality responsible for the collapse of northern cod? Can. J. Fish. Aquat. Sci. **52**: 1274–1285.

Nakashima, B. 1988. Capelin school surface index for NAFO Div. 3L 1982–1987. NAFO SCR. Doc 88/11 N1447.

Olsen, S., and Soldal, A.V. 1989. Observations on inshore distribution and behaviour of 0-group northeast Arctic cod. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **191**: 296–302.

Paloheimo, J.E., and Dickie, L.M. 1964. Abundance and fishing success. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **155**: 152–163.

Pope, J.G., and Garrod, D.J. 1975. Sources of error in catch and effort quota regulations with particular reference to variations in catchability coefficients. ICNAF Res. Doc. 81/36.

Radovich, J. 1976. Catch-per-unit-of-effort: fact, fiction or dogma. Mar. Res. Comm. Calif. Coop. Oceanic Fish. Invest. Rep. **18**: 31–33.

Radovich, J. 1979. Managing pelagic schooling fish species. *In* Predator–prey systems in fisheries management. *Edited by* H. Clepper. Sport Fisheries Institute, Washington, D.C. pp. 365–376.

Rastetter, E.B., King, A.W., Cosby, B.J., Hornberger, G.M., O'Neill, R.V., and Hobbie, J.E. 1992. Aggregating fine-scale ecological knowledge to model coarser-scale attributes of ecosystems. Ecol. Appl. **2**: 55–70.

Rose, G.A., and Leggett, W.C. 1991. Effects of biomass–range interactions on catchability of migratory demersal fish by mobile fisheries: an example of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **48**: 843–848.

Shaaf, W.E. 1980. An analysis of the dynamic population response of Atlantic Menhaden, *Brevoortia tyrannus* to an intensive fishery. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **177**: 243–251.

Sinclair, A. 1992. Fish distribution and partial recruitment: the case of eastern Scotian shelf cod. J. Northwest Atl. Fish. Sci. **13**: 15–24.

Swain, D.P. 1993. Age- and density-dependent bathymetric pattern of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**: 1255–1264.

Swain, D.P., and Sinclair, A.F. 1994. Fish distribution and catchability: what is the appropriate measure of distribution ? Can. J. Fish. Aquat. Sci. **51**: 1046–1054.

Swain, D.P., and Wade, E.J. 1993. Density-dependent geographic distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**: 725–733.

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

Tupper, M., and Boutelier, R. 1995. Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. Mar. Ecol. Prog. Ser. **118**: 295–300.

Tveite, S. 1984. 0-group cod investigations on the Norwegian Skagerrak coast. *In* The propagation of cod *Gadus morhua* L. *Edited by* E. Dahl, D.S. Danielssen, E. Moksness, and P. Solemdal. Flodevigen Rapp. **1**: 581–590.

Wigley, S.E., and Serchuk, F.M. 1992. Spatial and temporal distribution of juvenile Atlantic cod *Gadus morhua* in the Georges Bank – Southern New England region. Fish. Bull. **90**: 599–606.

Winters, G.H., and Wheeler, J.P. 1985. Interaction between stock area, stock abundance, and catchability coefficient. Can. J. Fish. Aquat. Sci. **42**: 989–998.

© 1997 NRC Canada

Appendix

Table A1. Fleming sites sampled during 1959–1964 and 1992–1994.

	Beach No.	Beach name	Longitude	Latitude
South	01	Harricot Beach	53°31.9′	47°10.1′
	02	Half Island	53°31.9′	47°11.1′
	03	Mother Hicks Cove	53°40.8′	47°00.7′
	04	Admirals Beach	53°38.8′	47°00.3′
	05	Mosquito Cove	53°41.1′	47°59.3′
	06	North Harbour (bottom)	53°38.9′	47°09.6′
	10	Trepassey	53°21.9′	46°45.1′
	12	Cape Broyle	52°52.8′	47°05.9′
Conception Bay	16	Davies Head (N)	53°15.7′	47°34.4′
	17	Davies Head (S)	53°15.6′	47°34.4′
	18	Crockers Cove	53°11.9′	47°44.6′
	19	Bryants Cove	53°11.3′	47°40.5′
	20	Bristols Hope Cove	53°11.7′	47°43.3′
Trinity Bay	25	Rantem Cove	53°55.4′	47°41.8′
	26	Masters Head	53°50.1′	47°43.1′
	27	Little Mosquito Cove	53°53.9′	47°50.5′
	28	Bald Point Beach	53°52.4′	47°50.4′
	29	Long Beach (E)	53°48.8′	47°59.8′
	30	Long Beach (W)	53°49.1′	47°59.8′
	31	Lower Lance Cove	53°41.6′	48°08.9′
	32	Middle Lance Cove	53°43.8′	48°09.1′
	33	Burgoynes Coves	53°42.4′	48°10.1′
	34	Lockston's Arm	53°22.3′	48°23.5′
	35	Cape Cove	53°22.2′	48°22.5′
Bonavista Bay	40	Cannings Cove	53°50.8′	48°26.7′
	41	Man Point	53°51.0′	48°25.7′
	42	Jamestown	53°47.7′	48°26.8′
	43	Great Chance Harbour (bottom)	53°42.0′	48°30.4′
	44	Great Chance Harbour (right)	53°41.8′	48°30.8′
	45	Eastport	53°45.6′	48°39.5′
	46	Indian Bay	53°46.6′	49°00.8′
New World Island and Gander Bay	50	Rubens Cove	54°25.6′	49°23.3′
	51	Grassy Island	54°24.8′	49°24.1′
	52	Seal Island	54°28.1′	49°26.0′
	53	Fox Island	54°28.7′	49°24.3′
	57	Bridgeport	54°49.7′	49°33.3′
	58	Luke's Arm	54°48.9′	49°31.3′
Notre Dame Bay	65	Fortune Harbour (NW, bottom)	55°17.0′	49°31.7′
	66	Fortune Harbour (Fox Cv. 1)	55°16.5′	49°31.5′
	67	Fortune Harbour (Fox Cv. 2)	55°16.5′	49°31.3′
	68	Fortune Harbour (SW bottom)	55°16.0′	49°30.5′
	69	Fortune Harbour (SE bottom)	55°13.0′	49°30.0′
	70	Wild Bight	55°41.2′	49°22.9′
	71	Julies Harbour	55°42.6′	49°26.8′
	72	Tommy's Arm	55°45.7′	49°28.3′
	75	Woodfords Arm (outcrops)	55°51.2′	49°31.3′
	76	Woodfords Arm (middle)	55°51.2′	49°31.2′
	77	Woodfords Arm (bottom)	55°51.2′	49°31.1′
	78	Lower Wolfe Cove	56°03.9′	49°29.5′
	79	Green Island	56°03.7′	49°29.3′
	80	Halls Bay, Beachy Cove	56°05.3′	49°28.0′
	81	Shimmey Cove	55°55.2′	49°36.4′
	82	Little Bay Arm	55°59.6′	49°34.3′
	83	Middle Arm (bottom)	55°55.5′	49°40.5′
	84	Middle Arm (Green Bay)	56°05.2′	49°41.8′
	85	King's Point (Green Bay)	56°09.9′	49°34.9′

© 1997 NRC Canada

Table A2. Duration of survey for juvenile cod by year and bay in eastern Newfoundland.

Area	1959	1960	1961	1962	1963	1964	1992	1993	1994
South	23 Sept.	12 Sept.	8 Sept.	17 Sept.	19 Sept.	18 Sept.	21 Sept.	21 Sept.	21 Sept.
	24 Sept.	20 Sept.	15 Sept.	22 Sept.	15 Sept.	25 Sept.	23 Sept.	23 Sept.	23 Sept.
CB	2 Oct.	28 Sept.	21 Sept.	26 Sept.	5 Oct.	24 Sept.	28 Sept.	28 Sept.	29 Sept.
	8 Oct.	29 Sept.	23 Sept.	27 Sept.	7 Oct.	25 Sept.	29 Sept.	29 Sept.	4 Oct.
TB	10 Oct.	3 Oct.	25 Sept.	1 Oct.	10 Oct.	29 Sept.	20 Sept.	30 Sept.	30 Sept.
	12 Oct.	4 Oct.	30 Sept.	14 Oct.	12 Oct.	3 Oct.	6 Oct.	6 Oct.	6 Oct.
BB	16 Oct.	6 Oct.	3 Oct.	11 Oct.	17 Oct.	6 Oct.	8 Oct.	8 Oct.	7 Oct.
		10 Oct.	7 Oct.	16 Oct.	19 Oct.	8 Oct.	9 Oct.	9 Oct.	8 Oct.
NWI-GB	23 Oct.	17 Oct.	9 Oct.	17 Oct.	21 Oct.	12 Oct.	14 Oct.	14 Oct.	14 Oct.
	26 Oct.	18 Oct.	13 Oct.	19 Oct.	31 Oct.	22 Oct.	15 Oct.	15 Oct.	
NDB	23 Oct.	17 Oct.	9 Oct.	17 Oct.	21 Oct.	12 Oct.	14 Oct.	14 Oct.	14 Oct.
	26 Oct.	27 Oct.	24 Oct.	26 Oct.	31 Oct.	22 Oct.	21 Oct.	21 Oct.	22 Oct.

Note: South, Saint Mary's Bay + Southern Shore; CB, Conception Bay; TB, Trinity Bay; BB, Bonavista Bay; NWI-GB, New World Island and Gander Bay; NDB, Notre Dame Bay.

© 1997 NRC Canada

Fish prey spectrum of short-finned squid (*Illex illecebrosus*) at Newfoundland

Earl G. Dawe, Edgar L. Dalley, and Wayne W. Lidster

Abstract: Fish otoliths were collected from stomachs of short-fined squid (*Illex illecebrosus*) at 11 coastal Newfoundland localities over 11 years during 1980–1993. Most oltoliths were of young-of-the-year Atlantic cod (*Gadus morhua*) and they were common at all localities after July. Adult capelin (*Mallotus villosus*) otoliths were common early in the season at a southern locality whereas otoliths of juvenile sand lance (*Ammodytes* sp.) were common later in the season at the northern localities. Other fish that were relatively well represented in only a few otolith collections were Arctic cod (*Boreogadus saida*), Atlantic herring (*Clupea harengus*), redfish (*Sebastes* sp.), and unidentified hake (Gadidae). Arctic cod otoliths were unusually prominent in only two years and from northernmost localities. Redfish otoliths were especially prevalent in the only collection from the south coast of Newfoundland. Paramount among the biases inherent in using this approach to estimate the effects of predation by squid on fish are apparent tendencies for squid not to consume the heads and otoliths when they prey upon large fish, and for otoliths to remain in stomachs for variable periods of time depending on their size or shape.

Résumé : Des otolithes de poissons ont été prélevés dans l'estomac de calmars à nageoires courtes (*Illex illecebrosus*) dans 11 sites sur la côte de Terre-Neuve, sur une période de 11 ans, de 1980 à 1993. La plupart des otolithes provenaient de jeunes morues franches (*Gadus morhua*) de l'année, et ils étaient répandus dans tous les sites après le mois de juillet. Les otolithes de capelans (*Mallotus villosus*) adultes étaient abondants au début de la saison dans un site situé au sud, alors que des otolithes de jeunes lançons (*Ammodytes* sp.) étaient répandus plus tard dans la saison dans les sites situés au nord. D'autres epèces de poissons qui étaient relativement bien représentées dans quelques-uns seulement des échantillons d'otolithes comprenaient la morue polaire (*Boreogadus saida*), le hareng atlantique (*Clupea harengus*), le sébastes (*Sebastes* sp.), de même que des merlus non identifiés (Gadidés). Les otolithes de morue polaire étaient anormalement abondants au cours de deux années seulement et dans les sites situés le plus au nord. Les otolithes de sébaste étaient particulièrement abondants dans le seul échantillon provenant de la côte sud de Terre-Neuve. Parmi les biais inhérents les plus importants à l'utilisation de cette méthode pour évaluer les effets de la prédation des calmars sur les poissons, il est essentiel de noter la tendance que semblent avoir les calmars à ne pas consommer les têtes et les otolithes lorsqu'ils se nourrissent de gros poissons, et le fait que les otolithes demeurent dans les estomacs des calmars pour des périodes variables, selon leur taille ou leur forme.
[Traduit par la Rédaction]

Introduction

Abundance of short-finned squid (*Illex illecebrosus*) in Northwest Atlantic fishery areas fluctuates greatly, especially in the most northern areas, on the Nova Scotian Shelf, and in Newfoundland coastal waters (Dawe and Warren 1993). Throughout the commercial fishery area, which extends between Cape Hatteras and Newfoundland, fish constitutes an important component of the diet of large squid (Maurer and Bowman 1985; Vinogradov and Noskov 1979; Amaratunga 1983; Squires 1957; Ennis and Collins 1979; Dawe 1988). However, squid macerate food during ingestion, so it is quite difficult to identify species. Therefore, only a few studies have reported some of the fish species consumed by squid on the U.S. Continental Shelf (Vinogradov and Noskov 1979; Froerman 1984), on the Nova Scotian Shelf (Vinogradov and Noskov 1979; Amaratunga 1983; Froerman 1984), and at Newfoundland (Squires 1957). These identifications have been based on miscellaneous hard structures of fish recovered from squid stomachs.

The only previous study that identified fish species preyed upon by squid at Newfoundland was that of Squires (1957). He noted fish species represented by eggs and various hard structures that were recovered from some 1500 squid stomachs sampled both inshore and on the edge of the Grand Bank during 1946–1952. However, that study provided little information on the relative importance of the various fish species to the squid diet and no estimates of prey size. Neither are there any data on geographic, seasonal, or annual variation in the fish prey spectrum. Such more-detailed studies are crucial to understanding the role of piscivorous short-finned squid in the ecosystem. When the Newfoundland commercial catch of short-finned squid peaked at 93 000 t in 1979, it was recognized that predation by short-finned squid could impose an important source of mortality on commercially important fish species, in some years. Furthermore, variation in the prominence of various fish species in the squid diet could potentially reflect shifts in availability or abundance of prey species.

Received March 7, 1995. Accepted December 8, 1995.
J13307

E.G. Dawe, E.L. Dalley and W.W. Lidster. Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.

© 1997 NRC Canada

Table 1. .Summary of sampling of squid stomachs for fish otoliths and the occurrence of otoliths in stomachs.

Year and locality	Months	No. of stomachs examined	No. with otoliths (%)	No. of otoliths	No. of otoliths per stomach[a]	No. of otoliths per all stomachs
1980						
Holyrood	July, Aug., Sept., Oct.	550	3 (0.5)	3	1.0	0.01
Twillingate	Aug., Sept., Oct.	734	32 (4.4)	138	4.3	0.19
LaScie	Aug., Sept.	681	75 (11.1)	317	4.2	0.47
1981						
Hermitage	July, Aug., Sept.	1 444	10 (0.7)	30	3.0	0.02
Holyrood	July, Aug., Sept.	2 040	59 (2.9)	166	2.8	0.08
Twillingate	Aug.	438	16 (3.6)	48	3.0	0.11
LaScie	Sept., Oct.	480	178 (37.1)	1052	5.9	2.20
1982						
Holyrood	July, Aug.	800	191 (23.9)	1110	5.8	1.39
LaScie	Aug., Sept.	561	42 (7.5)	146	3.5	0.26
Hampden	Sept., Oct.	393	290 (73.8)	2227	7.7	5.67
1985						
Holyrood	Aug., Sept.	616	32 (5.2)	56	1.8	0.09
St. Chad's	Oct.	149	16 (10.7)	41	2.6	0.28
1987						
Leading Tickles	Oct.	508	95 (73.6)	351	3.7	0.69
1988						
Holyrood	Sept.	202	39 (19.3)	115	2.9	0.57
1989						
Holyrood	July, Aug.	455	7 (1.5)	14	2.0	0.03
1990						
Holyrood	July, Aug., Sept.	612	62 (10.8)	108	1.7	0.18
Jackson's Arm	Aug., Sept., Oct.	1 050	211 (20.1)	940	4.5	0.90
1991						
Holyrood	Aug., Sept., Oct., Nov.	1 369	124 (9.1)	325	2.6	0.24
Jackson's Arm	Aug., Sept.	1 198	75 (6.3)	324	4.3	0.27
1992						
Holyrood	July, Aug., Sept.	2 669	283 (10.6)	604	2.1	0.23
1993						
New Bonaventure	Nov.	300	5 (1.7)	8	1.6	0.03
Chance Cove	Nov.	245	19 (7.8)	122	6.4	0.50
Bay d'Espoir	Oct.	235	4 (1.7)	6	1.5	0.03
Total		17 729	1868 (10.5)	8251		

[a]For only those stomachs containing otoliths.

Results of the first such comprehensive study, based on collection and identification of fish otoliths from squid stomachs since 1979, are presented here. Sources of variation in the fish prey spectrum are described, body sizes of those fish species most frequently identified are estimated, and the biases associated with interpreting prey composition based on occurrence of otoliths alone are addressed.

Methods

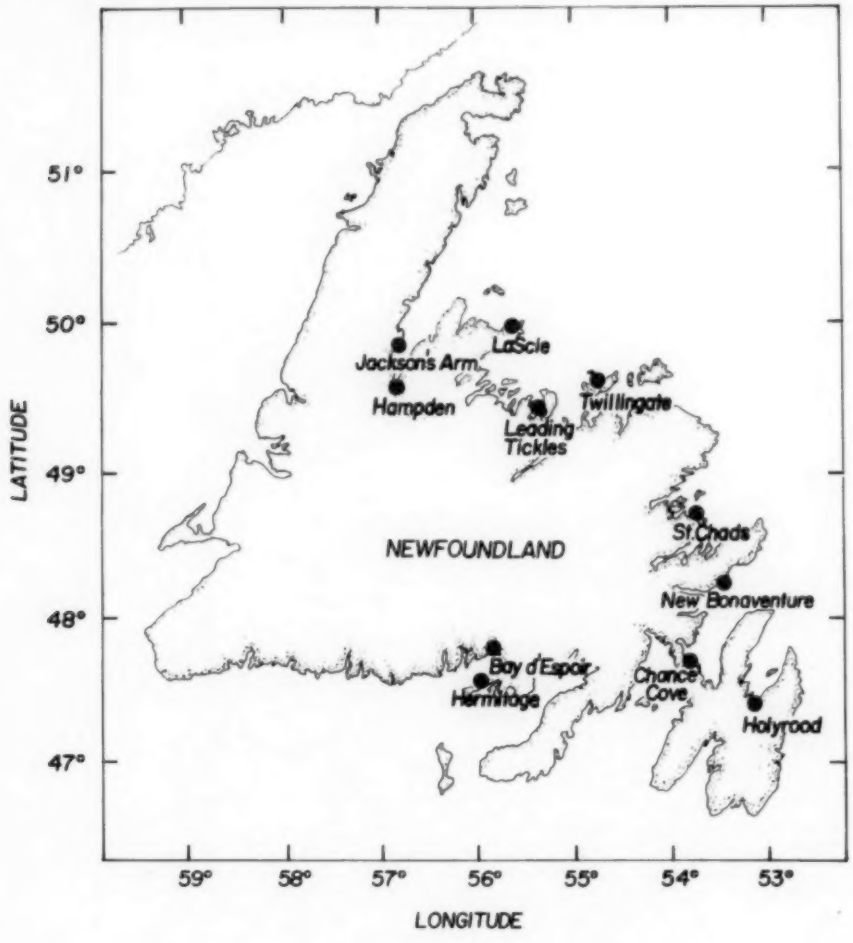
Randon samples of short-finned squid were acquired from the commercial jig fishery during 1980–1982, 1985, and 1987–1993 at various localities about insular Newfoundland (Table 1; Fig. 1). Samples were secured at 2-wk intervals, when available, at the regular sampling sites (Holyrood, LaScie, and Twillingate); but availability of squid was irregular and particularly low in recent years (Table 1). In some years of very low squid abundance, special effort was expended to sample squid at some of the few localities where they were fished, i.e., Hampden in 1982, St. Chad's in 1985, Leading Tickles in 1987, Jackson's Arm in 1990, and three new sampling sites in 1993 (Table 1; Fig. 1). Samples were either examined in fresh condition very soon after capture or were quick-frozen and subsequently thawed for analysis.

Detailed analysis of samples included estimation of dorsal mantle length (DML, centimetres) and examination of stomachs. Stomach fullness was assessed by employing an index that ranged from 1 (empty) to 6 (distended with food). Stomachs were opened and the contents identified (when possible) to general prey type, predominantly crustacean, fish, or cephalopod remains (Dawe 1988). Stomach contents were examined macroscopically but thoroughly to find and collect fish otoliths.

Otoliths were identified, to species level when possible (Lidster et al. 1994), and measured in maximum length, using an ocular micrometer, to the nearest 0.01 mm. Fish length was estimated from otolith length for the most commonly occurring otolith types by applying relationships developed for those species and this purpose (Lidster et al. 1994). Lengths represent total fish length for all species

© 1997 NRC Canada

Fig. 1. Map of insular Newfoundland showing localities where squid were sampled for stomach analysis.



except Atlantic cod (*Gadus morhua*), which was estimated in fork length.

Fish prey length frequency distributions were produced to represent the minimum number of fish of each species consumed, by recognizing possible otolith pairs, based on size, in each squid stomach. Fish length – otolith length relationships were not suitable for the smallest gadid otoliths collected from squid stomachs (Lidster et al. 1994). For those small otoliths, fish length was approximated by linear extrapolation to the origin from the size data for smallest gadids utilized in developing those relationships.

Results

Incidence of otoliths in squid stomachs

The percentage of short-finned squid stomachs containing otoliths was highly variable, ranging from less than 1 to 74% (Table 1). It was especially variable among sampling sites, generally increasing from the most southern sites of Hermitage and Holyrood (Fig. 1) to the more northern sampling sites. In only one of six years when such areal comparisons were possible was the percentage of stomachs containing otoliths lower at a more northern sampling site (LaScie in 1982) than at Holyrood or Hermitage (Table 1).

Yearly variation in percentage of stomachs with otoliths was considered at Holyrood, where data were available for seven years. Annual effects were less pronounced than were spatial effects. At Holyrood, stomachs with otoliths ranged from less than 1% in 1980 to 24% in 1982 (Table 1).

Overall, the mean number of otoliths per stomach, for those stomachs containing otoliths, ranged from 1.0 to 7.7 (Table 1) and was positively correlated with the percentage of stomachs containing otoliths (Spearman correlation coefficient = 0.72, $p = 0.001$). Because of this correlation, it was felt that the best single index of otolith occurrence was the mean number of otoliths for all stomachs examined (Table 1). The incidence of otoliths in squid stomachs at Hampden (Fig. 1) in 1982 was especially high at 5.7 otoliths per stomach for all stomachs examined (Table 1). One stomach contained 77 otoliths.

Locality effects on otolith occurrence were confounded with seasonal effects. Early (especially July) samples were

© 1997 NRC Canada

Table 2. Monthly mean number of otoliths per stomach (for all stomachs examined) by locality and year.

Locality and year	July	Aug.	Sept.	Oct.	Nov.
Bay d'Espoir					
1993				0.03	
Hermitgage					
1981	0	0.03	0.02		
Holyrood					
1980	0.06	0	0	0	
1981	0.03	0.09	0.64		
1982	0.05	1.84			
1985		0.02	0.17		
1988			0.57		
1989	0.01	0.12			
1990	0.18	0.16	0.24		
1991		0.06	0.26	0.48	0.10
1992	0.20	0.28	0.16		
Chance Cove					
1993					0.50
New Bonaventure					
1993					0.03
St. Chad's					
1985				0.28	
Twillingate					
1980		0.34	0	0.03	
1981		0.11			
Leading Tickles					
1987				0.69	
LaScie					
1980		0.33	0.52		
1981			2.78	0.94	
1982		0.05	1.31		
Hampden					
1982			8.71	2.73	
Jackson's Arm					
1990		0.44	1.93	0.71	
1991		0.32	0.24		

most commonly available from the southern localities of Hermitage and Holyrood whereas late (October–November) samples were most common from the more northern localities (Table 2). Seasonal inconsistency of sampling precluded rigid comparison among sampling sites by month. However, the July samples, when available, did appear to contribute to the low yearly incidence of otoliths in stomachs from those southern sites. For all seven July samples from Holyrood and Hermitage, the number of otoliths per stomachs ranged only from 0 to 0.20. It appears, despite sampling limitations, that the number of otoliths per stomach generally increased from July to September whereas it usually decreased from September to October (Table 2).

Although seasonal effects probably accounted for many of the differences among localities in otolith occurrence, a locality effect remained likely. Otolith occurrence appeared to be higher at the three most northwestern localities (LaScie, Hampden, and Jackson's Arm; Fig. 1) than at the others. The August–October monthly number of otoliths per stomach exceeded 0.9 in six of 13 collections (46%) at those three most northern localities whereas it exceeded 0.9 in only one of 25 collections (4%) from all other localities (Table 2). The incidence of otoliths was especially low at Hermitage, the most southern locality, in 1981.

Species composition of otoliths

Great variability was evident in the species composition of otolith collections from stomachs sampled in different localities and years (Table 3). Atlantic cod otoliths predominated overall, representing 61% of all otoliths and being present in all collections except 1980. Atlantic cod represented the most common otoliths in 11 of 17 collections (65%) during 1980–1990, but only in two of six collections (33%) during 1991–1993.

Sand lance (*Ammodytes* sp.) otoliths were the second most common type, representing 16% of all otoliths collected. They represented the most abundant otolith type in stomachs from Leading Tickles in 1987 (23%) and from Holyrood in 1991 (49%).

Arctic cod (*Boreogadus saida*) otoliths represented 8% of

© 1997 NRC Canada

Table 3. Breakdown by lowest taxonomic level possible of fish otoliths found in squid stomachs at inshore Newfoundland localities during 1980–1993 (values in parentheses represent percentages by taxon of otoliths found).

Year and locality	No. of stomachs examined	No. of otoliths	Number of otoliths per taxon						
			Atlantic cod	Sand lance	Arctic cod	Capelin	Hake	Atlantic herring	Other
1980									
Holyrood	550	3	—	—	—	—	—	—	3 (100)
Twillingate	734	138	—	—	116 (84)	—	—	—	22 (16)
LaScie	681	317	—	—	317 (100)	—	—	—	—
1981									
Hermitage	1 444	30	14 (47)	—	—	—	—	—	16 (53)
Holyrood	2 040	166	133 (80)	—	—	16 (10)	1 (<1)	—	16 (10)
Twillingate	438	48	46 (96)	—	—	1 (2)	—	—	1 (2)
LaScie	480	1052	692 (65)	309 (29)	35 (3)	3 (<1)	—	—	13 (1.2)
1982									
Holyrood	880	1110	1088 (98)	—	—	20 (2)	—	—	2 (<1)
LaScie	561	146	109 (75)	36 (25)	—	—	—	—	1 (<1)
Hampden	393	2227	1514 (68)	649 (29)	—	3 (<1)	—	29 (1)	32 (2)
1985									
Holyrood	616	56	15 (27)	—	—	25 (45)	—	—	16 (28)
St. Chad's	149	41	22 (54)	15 (37)	—	—	—	—	4 (9)
1987									
Leading Tickles	508	351	75 (21)	81 (23)	2 <1)	—	1 (<1)	18 (5)	174 (50)
1988									
Holyrood	202	115	103 (90)	3 (3)	—	1 (1)	1 (1)	—	7 (4)
1989									
Holyrood	455	14	9 (64)	—	—	4 (29)	—	—	1 (7)
1990									
Holyrood	612	108	71 (65)	1 (1)	—	16 (15)	14 (13)	1 (1)	5 (5)
Jackson's Arm	1 050	940	774 (82)	66 (7)	41 (4)	28 (3)	—	2 (<1)	29 (4)
1991									
Holyrood	1 369	325	92 (28)	158 (49)	—	19 (6)	2 (<1)	19 (6)	35 (11)
Jackson's Arm	1 198	324	150 (46)	6 (2)	151 (47)	6 (2)	—	5 (1)	6 (2)
1992									
Holyrood	2 669	604	20 (3)	20 (3)	—	302 (50)	245 (41)	—	17 (3)
1993									
New Bonaventure	300	8	8 (100)	—	—	—	—	—	—
Chance Cove	245	122	122 (100)	—	—	—	—	—	—
Bay d'Espoir	235	6	1 (17)	—	—	5 (83)	—	—	—
Total	17 729	8251	5058 (61)	1344 (16)	662 (8)	449 (3)	264 (5)	74 (3)	400 (5)

© 1997 NRC Canada

Table 4. Percentages of monthly otolith collections represented by each of the three most prominent fish prey species (1980 not included because none of these species occurred then) (dashes indicate that no otoliths of a species were recovered for all months sampled).

	Capelin					Atlantic cod					Sand lance				
Locality and year	July	Aug.	Sept.	Oct.	Nov.	July	Aug.	Sept.	Oct.	Nov.	July	Aug.	Sept.	Oct.	Nov.
Bay de'Espoir															
1993				83					17					—	
Hermitage															
1981	—	—	—			0	50	14			—	—	—		
Holyrood															
1981	57	4	0			19	87	97			—	—	—		
1982	100	0.1				0	99				—	—			
1985		20	47				0	29				—	—		
1988			0.9					90					3		
1989	100	17				0	75				—	—			
1990	48	4	0			3	93	79			0	0	4		
1991		70	0	0	0		11	82	25	33		7	9	59	30
1992	95	30	73			0	0	15			0	2	8		
Chance Cove															
1993					—					100					—
New Bonaventure															
1993					—					100					—
St. Chad's															
1985				—					54					37	
Twillingate															
1981		2					96					—			
Leading Tickles															
1987				—					21					23	
LaScie															
1981			0.3	0				73	17				24	63	
1982		—	—				22	85				78	15		
Hampden															
1982			0.2	0				60	92				38	2	
Jackson's Arm															
1990		10	2	0			79	93	66			0	2	19	
1991		5	0				2	76				2	2		

all otoliths collected, but they were prevalent and predominant only from three northern collections during 1980 and 1991. Arctic cod otoliths were strikingly absent from Holyrood collections in those years. Three smaller Arctic cod collections, each representing less than 5% of the total, were also from northern localities (Table 3; Fig. 1).

Capelin (*Mallotus villosus*) otoliths represented 5% of all otoliths and were most prevalent at Holyrood, being absent from only one collection, that in 1980. They represented 10–50% of the total in five of the nine Holyrood collections. At all other sites, capelin otoliths were uncommon, not exceeding 3% of collections (excepting the 1993 Bay d'Espoir collection).

Otoliths of unspecified hake (Gadidae) represented 4% of all otoliths collected. All but one of these otoliths were recovered from Holyrood stomachs, mostly (93%) during 1992.

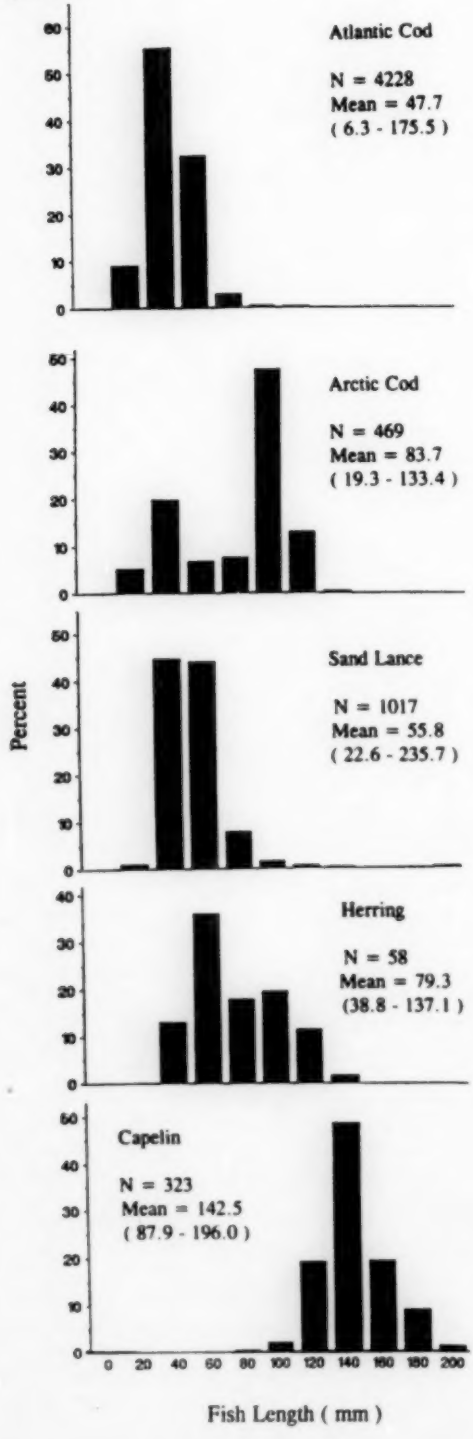
Atlantic herring (*Clupea harengus*) otoliths occurred but were uncommon (≤6% of otoliths) in six collections.

Otoliths of "other" species represented more than 10% of only six collections (Table 3). This group was composed entirely of redfish (*Sebastes* sp.) otoliths from Hermitage, in 1981, representing 53% of otoliths in that collection. Gadid otoliths that could not be assigned to species are included in this group. Other uncommon otoliths contributing to this group included five grenadiers (Macrouridae), two Greenland cod (*Gadus ogac*), one Atlantic halibut (*Hippoglossus hippoglossus*), one haddock (*Melanogrammus aeglefinus*), and one salmonid (Salmonidae). "Other" otoliths also included those that remained unidentified, at least to the family level.

The relative importance of spatial versus seasonal effects on occurrence of otoliths in squid stomachs was considered for each of the three species most commonly represented in the various collections (Table 4). Capelin otoliths were most prominent at Holyrood, early in the season, especially in July, representing 48–100% of all (except 1980) July collections. They were well represented in September collections only during 1985 and 1992 at Holyrood, and they were present in only one of six collections in October–November when, at Bay d'Espoir in 1993, only five capelin otoliths represented 83% of the total collection. Monthly collections of capelin

© 1997 NRC Canada

Fig. 2. Distribution of length, based on otoliths recovered from squid stomachs, for five fish species (fork length for Atlantic cod, total length for all other species). Ranges of length are given in parentheses. Two specimens of sand lance larger than 210 mm are not represented.



otoliths were too limited and variable to identify any spatial effects. It was noted, however, that no capelin otoliths were recovered from the single Hermitage collection, despite sampling of stomachs throughout July–September of 1981 and the occurrence of capelin otoliths in stomachs from three other localities in that year.

Atlantic cod otoliths were relatively uncommon in the July collections from the two most southern localities, representing only 0–19% of the Hermitage and Holyrood July collections (Table 4). They increased in prominence greatly from July to August in five of six cases and generally represented a major proportion of monthly otolith collections throughout August–November. Only in 1985 and 1992 at Holyrood were no Atlantic cod otoliths represented in August collections. No spatial effects were evident.

Sand lance otoliths were more common at the six most northern localities than at the five more southern localities (Table 4; Fig. 1). Indeed, they were present in only eight of 26 monthly collections from those five most southern localities and represented more than 9% of those monthly collections only in October and November of 1991 at Holyrood. They were usually present and frequently prevalent within the August–October collections from the more northern localities (St. Chad's to Jackson's Arm). Their prevalence appeared to increase throughout the season, but more extensive sampling will be required to conclusively determine seasonal effects.

Fish size composition from otoliths

The estimated body size (fork length) of Atlantic cod represented by otoliths was similar among sampling sites and years. It ranged from 6 to 176 mm overall, but only a few specimens were larger than 90 mm (Fig. 2).

Arctic cod ranged from 19 to 133 mm in total length but were mostly within the 70–130 mm range (Fig. 2), especially in 1980. The fewer otoliths collected in other years (Table 4) represented smaller fish and accounted for a secondary mode at 30–50 mm (Fig. 2).

The total length of sand lance estimated from otoliths ranged from 23 to 236 mm, but very few fish larger than 90 mm were represented (Fig. 2). There were no apparent differences in sand lance size composition among years or sampling sites.

Atlantic herring, overall, ranged from 39 to 137 mm (Fig. 2). Although otolith collections were limited, estimated Atlantic herring total lengths were clearly smaller at Hampden in 1982 (mostly 50–70 mm) than at Leading Tickles in 1987 (mostly 90–110 mm). This accounts for the observed bimodality in the pooled length frequency.

Otoliths of capelin ingested by squid represented bigger fish than did otoliths of any other species (Fig. 2). These included adult capelin, ranging from 88 to 196 mm in total length.

Discussion

The fish prey spectrum of short-finned squid at Newfoundland is typical of other adult ommastrephids and of pelagic teuthoid squids in general (Wormuth 1976; Breiby and Jobling 1985; reviewed by Nixon 1987). Pelagic adult squids are generally opportunistic piscivores that probably prey on whatever fish is available within a suitable size range. Squires (1957) identi-

© 1997 NRC Canada

fied eggs and a variety of hard structures from squid stomachs collected within the Newfoundland area (including offshore samples). He found that capelin and redfish predominated, with other fish consisting of Atlantic cod, haddock, ribbed sculpin (*Triglops pingeli*), and small flounders (Pleuronectidae). Identifiable hard structures of fish in squid stomachs sampled between the Scotian Shelf and Cape Hatteras were mostly of silver hake (*Merluccius bilinearis*), lanternfishes (Myctophidae), and unknown gadids (Amaratunga 1983; Froerman 1984; Vinogradov and Noskov 1979). Other fishes that were less common included white barracudina (*Notolepis rissoi*), longfin hake (*Urophycis chesteri*), ocean pout (*Macrozoarces americanus*), redfish (*Sebastes marinus*), and unidentified representatives of the families Astronesthidae, Gonostomatidae, Macrouridae, and Chilodipteridae.

Previous studies have shown that when short-finned squid first arrive in coastal Newfoundland waters, typically in July, their diet shifts from mostly crustaceans to predominately fish (Squires 1957; Ennis and Collins 1979). Piscivory appears to be particularly prevalent in July, with cannibalism becoming common in later months (Ennis and Collins 1979). Although piscivory is generally most common in July, our study found the occurrence of otoliths in squid stomachs to be relatively low in that month, with adult capelin predominating among those otoliths collected.

The extent of predation on capelin early in the season may not be well reflected by the otolith collections. When squid prey on abundant and relatively large fish such as adult capelin, they probably consume soft tissue and reject the head and skeleton, as is common in teuthoid squids (Nixon 1987). O'Dor et al. (1980) noted that this feeding behaviour was common in short-finned squid in captivity when they were feeding on live *Fundulus* sp. of mostly 6–11 cm in length. Intact heads and skeletons of large fish of various species are commonly observed at Newfoundland in live traps when short-finned squid are present (personal observation). Froerman (1984) found evidence that squid usually do not consume skeletal material when preying on large fish even when they are not confined. It is also recognized, however, that sharing of large fish by schooling predators may also contribute to low consumption of otoliths when squid prey on capelin. We calculated, as an index of otolith ingestion, the percentage of those stomachs containing fish flesh that also contained otoliths. This index ranged from 0 to 58% but showed no clear effects of year, month, or locality. Squires (1957) found, by identifying eggs and various skeletal material, that capelin was the most common fish prey of large inshore squid. Clearly, capelin serves as an important prey of short-finned squid at Newfoundland. This opposes the assertion of Leggett and Frank (1990) that short-finned squid and capelin are competitors in Newfoundland inshore waters. That hypothesis was based on an apparent inverse relationship between abundances of capelin and squid as well as assumed similarity in their diets. However, that inverse relationship can be as equally well explained by predation as by competition. Furthermore, the diets of planktivorous capelin and predatory squid are obviously not similar in Newfoundland inshore waters.

Predation on Atlantic cod of the current year-class (0-group) appeared to be prevalent after July and was probably well represented by the otolith collections. Such small fish are probably consumed in their entirety. It is unknown whether the low occurrence of their otoliths in July was related to low availability of 0-group cod or to an abundance of preferred adult capelin. It may be that 0-group Atlantic cod are not usually available in coastal waters as early as July. Atlantic cod early life history is poorly known, but, supposedly, spawning, at least of cod in NAFO Divisions 2J3KL, extends from March to June, with settlement (largely in bays of northeastern Newfoundland) occurring at sizes of 25–60 mm (Brown et al. 1989; Lear and Green 1984; Helbig et al. 1992). This suggests that squid may prey mostly upon pelagic 0-group cod and that this prey is not usually available in inshore areas until August. It is noted that only in 1985 and 1992, when capelin otoliths were unusually prevalent in September, were Atlantic cod otoliths absent from Holyrood August collections. This could reflect selection by the predator, or alternatively extended inshore availability of capelin and delayed hatching of Atlantic cod in two unusually cold years. Although only a few otoliths of Atlantic cod between 90 and 176 mm in fork length were collected, it is recognized that such relatively large cod may be preyed upon but without consumption of their otoliths.

Some spatial effects were apparent. Occurrence of otoliths in general was highest at the most northern localities where 0-group Atlantic cod and sand lance (probably 0-group and 1-group (Winters 1981)) represented most of the collection. It was lower at Holyrood, where Atlantic cod and capelin predominated. It was, by far, the lowest in the single Hermitage collection where redfish and Atlantic cod represented virtually all of the small collection. It appears that availability of suitable fish prey is low at that southern locality, where the diet is predominated by crustaceans (Ennis and Collins 1979). This is despite the fact that young sand lance are known to occur within bays on the south coast of Newfoundland (Dalley and Winters 1987).

Annual effects on composition of otolith collections were evident, with the 1980 collection being unusual. In that year, otoliths were virtually absent from stomachs collected at Holyrood although squid preyed heavily on fish in July (Dawe 1988). All identifiable otoliths from more northern localities were of Arctic cod. In both 1980 and 1991, Arctic cod otoliths represented an important component of the otolith collections from northern localities whereas they were absent from Holyrood. The high occurrence of sand lance, relative to Atlantic cod, otoliths at Holyrood in 1991 may be related to late sampling. It is not known whether the high prevalence of hake otoliths at Holyrood in 1992 was due to high abundance of juvenile hake or low abundance of Atlantic cod.

Arctic cod and Atlantic herring otoliths represented larger fish than did those of Atlantic cod and sand lance. It may be that these relatively large fish are more commonly preyed upon by squid than our study suggests, if their otoliths are not usually consumed. It is also possible that even larger fish may be preyed upon by squid but their otoliths are not ingested. Adult Atlantic saury (*Scomberesox saurus*), for example, are frequently abundant in coastal areas, including at Holyrood. They are commonly eaten by short-finned squid (except head and skeleton) when these species co-occur in live traps (personal observation). It remains unknown, however, if these large fish are subject to predation by squid when at liberty. O'Dor et al. (1980) directly observed that short-finned squid

© 1997 NRC Canada

in captivity preyed upon fish as large as the predator's mantle length and were not apparently selective below that size. However, Froerman (1984) only rarely found hard structures in squid stomachs that corresponded to fish as large as 12–20 cm mantle length, generally agreeing with our study.

Determining the true species composition of fish in the squid diet based on otoliths, or any hard structures, would be difficult. As ready noted, otoliths are probably not usually ingested when squid prey on relatively large fish, such as capelin, and schooling squid probably share large fish. An opposing bias is that of otolith retention in stomachs. Larger capelin otoliths at Holyrood (and perhaps redfish otoliths at Hermitage) could remain in stomachs for a considerable period of time after other food has been digested. Digestion of organic matter is quite rapid, usually requiring about 16 h, when squid prey on fish. However, digestion of inorganic material, including otoliths, is probably slow, since stomach pH does not fall much below 5.5 (Wallace et al. 1981). Retention of otoliths in squid stomachs may be high because, unlike fishes, squid have a nonlinear digestive system. Flesh can be diverted to the caecum for digestion without pushing otoliths through the intestine. It is not known to what extent the size or shape of otoliths may affect retention of otoliths in stomachs. We calculated, as an index of otolith retention, the percentage of those stomachs containing otoliths that contained no other food material. This index ranged from 0 to 100% and showed no clear effects of year, month, or locality.

Eventually quantifying predation by short-finned squid on various fish species would be further complicated by unknown effects of variation in the relative abundance of squid and its various fish prey species. For example, it is not known to what extent the absence of otoliths of all species but Arctic cod in 1980 may have been due to an abundance of Arctic cod, unavailability of other species, or the high abundance of squid at Newfoundland in that year (Dawe and Warren 1993). Variation in size of available fish may also affect the status of any given species as a preferred prey. The effects of selectivity of sampling gear would also have to be considered. It seems likely that jigging devices, such as those used in our study, may selectively attract squid that had not recently fed. However, the selectivity of such sampling gear is not yet known.

The prospect of successfully addressing all the potential biases associated with studies such as ours seems unlikely. Perhaps, however, the problem of squid not ingesting otoliths when they prey on fish can be addressed by identifying soft tissue in squid stomachs using serological techniques (Grisley 1985; Grisley and Boyle 1985).

Acknowledgements

We thank Paul Beck, Joe Drew, Pat Veitch, Elaine Seward, and Cynthia Hickey for their assistance in summarizing and illustrating the data. Paul Beck and Joe Drew also examined most of the stomachs. Comments provided by R.K. O'Dor and another anonymous reviewer were constructive and appreciated. Thanks also go to Moira Hynes for preparing and revising the manuscript.

References

Amaratunga, T. 1983. The role of cephalopods in the marine ecosystem. *In* Advances in assessment of world cephalopod resources. *Edited by* J.F. Caddy. FAO Fish. Tech. Pap. **231**: 379–415.

Breiby, A., and Jobling, M. 1985. Predatory role of the flying squid (*Todarodes sagittatus*) in North Norwegian waters. NAFO Sci. Counc. Stud. **9**: 125–132.

Brown, J.A., Pepin, P., Methven, D.A., and Somerton, D.C. 1989. The feeding, growth and behavior of juvenile cod, *Gadus morhua*, in cold environments. J. Fish Biol. **35**: 373–380.

Dalley, E.L., and Winters, G.H. 1987. Early life history of sand lance (*Ammodytes*), with evidence for spawning of *A. dubius* in Fortune Bay, Newfoundland. Fish. Bull. **85**: 631–641.

Dawe, E.G. 1988. Length–weight relationships for short-finned squid in Newfoundland and the effect of diet on condition and growth. Trans. Am. Fish. Soc. **117**: 591–599.

Dawe, E.G., and Warren, W.G. 1993. Recruitment of short-finned squid in the Northwest Atlantic Ocean and some environmental relationships. J. Ceph. Biol. **2**(2): 1–21.

Ennis, G.P., and Collins, P.W. 1979. Food and feeding of the short-finned squid, *Illex illecebrosus*, during its seasonal occurrence in the Newfoundland Area. ICNAF Sel. Pap. **5**: 25–29.

Froerman, Yu.M. 1984. Feeding spectrum and trophic relationships of short-finned squid (*Illex illecebrosus*) in the Northwest Atlantic. NAFO Sci. Counc. Stud. **7**: 67–75.

Grisley, M.S. 1985. The use of serological techniques for gut-content analysis in cephalopods. Rapp. Comm. Int. Mer. Mediterr. **29**: 221–226.

Grisley, M.S., and Boyle, P.R. 1985. A new application of serological techniques to gut-content analysis. J. Mar. Biol. Ecol. **90**: 1–9.

Helbig, J., Mertz, G., and Pepin, P. 1992. Environmental influences on the recruitment of Newfoundland/Labrador cod. Fish. Oceanogr. **1**: 39–56.

Lear, W.H., and Green, J.M. 1984. Migration of the 'northern' Atlantic cod and the mechanisms involved. *In* Mechanisms of migration in fishes. *Edited by* J.D. McCleave, G.P. Arnold, J.J. Dodson, and W.H. Neill. Plenum Press, New York. pp. 159–178.

Leggett, W.C., and Frank, K.T. 1990. The spawning of the capelin. Sci. Am. May 1990. pp. 102–107.

Lidster, W., Lilly, G.R., and Dawe, E.G. 1994. Otoliths of Arctic cod (*Boreogadus saida*), small Atlantic cod (*Gadus morhua*), and three other fish species from Newfoundland waters: description and relationship of fish length to otolith length. J. Northwest Atl. Fish. Sci. **16**: 33–40.

Maurer, R.O., and Bowman, R.E. 1985. Food consumption of squids (*Illex illecebrosus* and *Loligo pealei*) off the northeastern United States. NAFO Sci. Counc. Stud. **9**: 117–124.

Nixon, M. 1987. Cephalopod diet. *In* Cephalopod life cycles. Vol. 2. Comparative reviews. *Edited by* P.R. Boyle. Academic Press Inc. (London) Ltd., London. pp. 201–219.

O'Dor, R.K., Durward, R.D., Vessey, E., and Amaratunga, T. 1980. Feeding and growth in captive squid, *Illex illecebrosus*, and the influence of food availability on growth in the natural population. ICNAF Sel. Pap. **6**: 15–21.

Squires, H.J. 1957. Squid, *Illex illecebrosus* (LeSueur), in the Newfoundland fishing area. J. Fish. Res. Board Can. **14**: 693–728.

Vinogradov, V.I., and Noskov, A.S. 1979. Feeding of short-finned squid, *Illex illecebrosus*, and long-finned squid, *Loligo pealei*, off Nova Scotia and New England, 1974–75. ICNAF Sel. Pap. **5**: 31–36.

Wallace, I.C., O'Dor, R.K., and Amaratunga, T. 1981. Sequential observations on the digestive process in the squid, *Illex illecebrosus*. NAFO Sci. Counc. Stud. **1**: 65–69.

Winters, G.H. 1981. Growth patterns in sand lance, *Ammodytes dubius*, from the Grand Bank. Can. J. Fish. Aquat. Sci. **38**: 841–846.

Wormuth, J.H. 1976. The biogeography and numerical taxonomy of the oegopsid squid family Ommastrephidae in the Pacific Ocean. Bull. Scripps Inst. Oceanogr. **23**: 1–90.

© 1997 NRC Canada

Pup production and population growth of hooded seals (*Cystophora cristata*) near Newfoundland, Canada

G.B. Stenson, R.A. Myers, I-H. Ni, and W.G. Warren

Abstract: Pup production of hooded seals (*Cystophora cristata*) in two whelping concentrations along the northeast coast of Newfoundland (the "Front") during March 1990 was estimated using systematic visual surveys. In addition, independent estimates of production in one of the concentrations and the number of pups born outside the whelping concentrations were obtained from photographic surveys. Photographic estimates were adjusted for incorrectly identified pups by comparing black and white photographs with ultraviolet imagery. Estimates were also corrected for pups that had yet to be born at the time of the survey or had left the ice using distinct age-related developmental stages. Approximately 91% of the pups born in the first whelping concentration, and 92% born in the second, were present during the surveys. Based on a combination of visual and photographic surveys, the corrected pup production in these concentrations was estimated to be 49 600 (SE = 2700). Photographic surveys resulted in an estimate of 33 500 (SE = 12 400) pups born outside the whelping patches, although this estimate could not be corrected for the abscence of pups due to the temporal distribution of births. Thus, total pup production was estimated to be 83 100 (SE = 12 700). Although nominally greater, this estimate is not statistically different from a comparable estimate of hooded seal pup production in 1984.

Résumé : À l'aide de relevés visuels systématiques, nous avons estimé la production de petits chez les phoques à capuchon (Cystophora cristata) dans deux aires de mise bas le long de la côte nord-est de Terre-Neuve (le « Front ») au cours du mois de mars 1990. De plus, des estimations indépendantes de la production dans l'une des aires ainsi que le nombre de petits nés à l'extérieur de la mouvée ont été obtenus à partir de relevés photographiques. Pour tenir compte des petits incorrectement identifiés, les estimations photographiques ont été ajustées par comparaison des photos noir et blanc avec des images prises dans l'ultraviolet. En tenant compte des stades de développement distincts liés à l'âge, nous avons également corrigé les estimations pour tenir compte des petits qui étaient encore à naître au moment de l'étude, et de ceux qui avaient quitté la banquise. Environ 91% des petits nés dans la première aire de mise bas, et 92% de ceux nés dans la deuxième aire, étaient présents au cours des relevés. En nous basant sur une combinaison de relevés visuels et photographiques, nous avons estimé la production de petits dans ces aires, après correction, à 49 600 (ET = 2 700). Les relevés photographiques ont fourni une estimation de 33 500 (ET = 12 400) petits nés à l'extérieur des mouvées; cette valeur estimative n'a pas pu être corrigée pour tenir compte de l'absence de petits causée par la distribution des naissances dans le temps. Par conséquent, la production totale de petits a été estimée à 83 100 (ET = 12 700). Bien que très légèrement supérieure, cette valeur estimative n'est pas statistiquement différente d'une valeur comparable obtenue en 1984 pour la production de petits chez les phoques à capuchon.
[Traduit par la Rédaction]

Introduction

The hooded seal (*Cystophora cristata*) is one of the most abundant pelagic phocids in the North Atlantic. Although some give birth (whelp) on the pack ice in the eastern Atlantic near Jan Mayen Island (north of Iceland), the majority are found in the western Atlantic where they undergo annual migrations between whelping areas along the coast of Canada and in Davis Strait and moulting and summering areas off southeast and west Greenland. In the Northwest Atlantic, whelping occurs in the Davis Strait, off Newfoundland, and in Gulf of St. Lawrence. Of these, the largest number of whelping seals are found off the coast of southern Labrador or northern Newfoundland (the "Front") where, using catch data, researchers estimated pup production to be approximately 30 000 in the late 1960's (Øritsland and Benjaminsen 1975; Sergeant 1976; Lett 1977; Winters and Bergfløt 1978). In 1984, pup production at the Front was estimated to be 62 000 (95% CI 43 700 – 89 400; Bowen et al. 1987), based on aerial surveys. Although not directly comparable due to the different techniques used, this estimate was substantially higher than earlier ones, suggesting that either the population was increasing or the previous estimates were negatively biased.

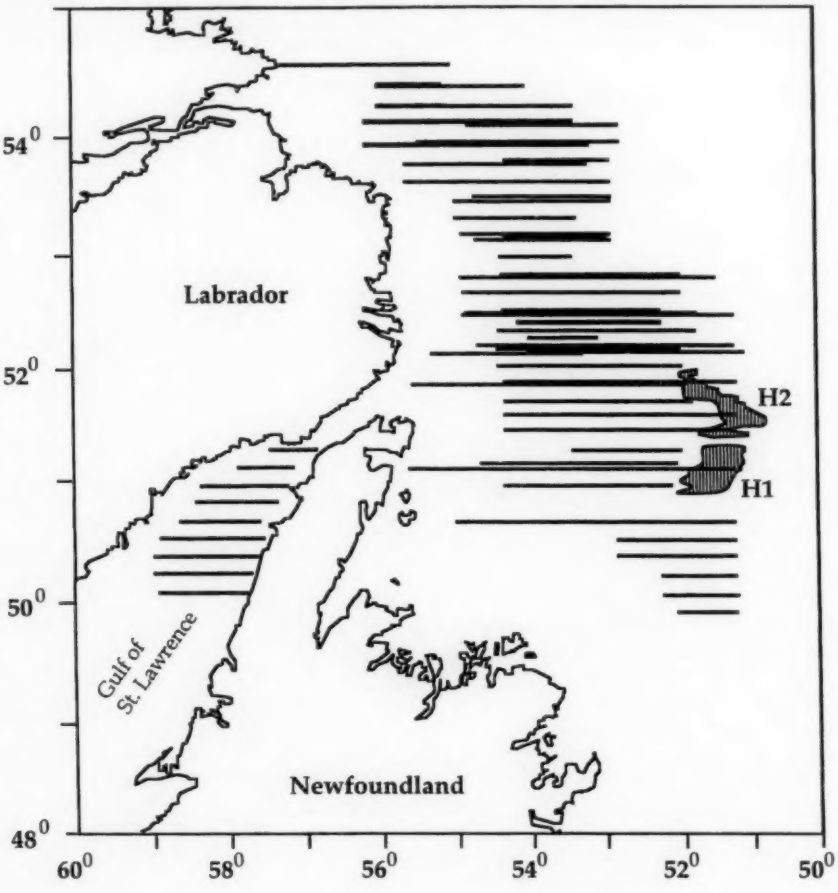
Commercial hunting of hooded seals at the Front has been reported since the nineteenth century, but likely occurred earlier. Between 1974 (when quotas were first introduced) and 1982, the average annual harvest was 12 500 animals, the

Received February 15, 1995. Accepted April 3, 1996.
J13446

G.B. Stenson, R.A. Myers, and W.G. Warren. Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.
I-H. Ni. Department of Biology, Hong Kong University of Science and Technology, Clearwater Bay, Kowloon, Hong Kong.

© 1997 NRC Canada

Fig. 1. Reconnaissance survey transects flown during March 1990. Hatching indicates location of whelping concentrations.



majority being pups taken by large vessels at the whelping concentrations (Anonymous 1995). Following the end of this hunt in 1983, commercial catches declined to an average of approximately 550 seals per year between 1983 and 1990. This decline in hunt-related mortality may have resulted in an increased population since the 1984 survey.

In addition to understanding hooded seal population dynamics, estimates of abundance are also necessary before we can determine their potential impact on fish stocks in the Northwest Atlantic. Hooded seals inhabit the Newfoundland continental shelf for much of the winter and spring (Stenson and Kavanagh 1994; G.B. Stenson, unpublished data) where they feed on a variety of commerically important fish such as Greenland halibut (*Reinhardtius hippoglossoides*), redfish (*Sebastes* spp.), and Atlantic cod (*Gadus morhua*) (Stenson et al. 1991; Ross 1992; Lawson et al. 1994), which declined in abundance in recent years (Sinclair 1993; Bishop et al. 1994; Bowering et al. 1994; Morgan et al. 1994; Power 1994). An accurate estimate of abundance is one of the requirements needed to quantify consumption of these prey by hooded seals.

The objective of this study was to estimate pup production of hooded seals at the Front during 1990 using a combination of visual and photographic surveys and, by comparison with earlier estimates, to determine if pup production had changed since the end of the commercial hunt for young hooded seals.

Methods

Identification of whelping areas

Reconnaissance surveys of the area historically used by whelping hooded seals were carried out to locate whelping concentrations. The area between 54°N and 49°N was surveyed between March 5 and 25 using using two Piper Navajo aircraft equipped with a LORAN C navigation system (Fig. 1). Systematic east–west transects, spaced 18.5 km apart, were flown at an altitude of 230 m from the coastal margin of the ice pack to the outer edge. Two observers, one per side, examined all ice considered thick enough to support seals (>30 cm thick). To account for ice drift and the wide range of pupping dates (early to late March), some areas were surveyed more than once. This design was expected to locate all of the major whelping concentrations which are generally >9 km in width (Bowen et al. 1987). When a whelping concentration was located, satellite and VHF radio transmitters were placed on the ice near or within the concentration to facilitate relocation and monitor movements.

© 1997 NRC Canada

Table 1. Regression statistics used to correct for misidentified pups on photographs taken during surveys of hooded seals off Newfoundland, 1990.

	No. of photographs	Intercept	Slope	r^2
Concentration H2	158	0.035 (0.022)	0.964 (0.032)	0.85
Stratum 2				
March 13	1111	0.019 (0.008)	0.521 (0.015)	0.52
March 20	267	0.007 (0.005)	0.591 (0.012)	0.90

Note: Surveys in Stratum 2 were used to estimate pup production outside the whelping concentrations. Standard errors are included in parentheses.

Estimates of abundance

Visual surveys

The number of pups present within the whelping concentrations was estimated by conducting visual strip transect surveys using a MMB105 helicopter equipped with a LORAN C navigation system and radar altimeter. Using laptop computers, two observers counted the number of pups present within known strips on each side of the helicopter. Survey strips were defined by placing reference marks on the windows using a known distance marked on the ice. Additional marks were placed at the level of the horizon and in line with the edge of the helicopter floats to help observers keep their heads in the same position throughout the surveys. A navigator, seated beside the pilot, directed the survey and ensured that transect lines were flown correctly. Ground speed was maintained at the minimum possible (≤80 km/h) to maximize the viewing time and ensure complete counts.

For each survey, the first transect was flown along the first whole minute of latitude closest to one edge of the concentration. Each transect began before any seals were encountered and was terminated when no seals were seen over a distance of approximately 5 km. The survey ended when no seals were seen along a transect and could not be observed outside the survey area.

Two whelping concentrations were surveyed. The first (H1) was surveyed on March 21 at a flying altitude of 92 m with a total survey width of 400 m (200 m per observer) per transect. Transects were spaced 1.85 km apart for the first 17 transects but increased to 3.7 km for the final seven transects to ensure that the entire concentration was surveyed in a single day. The second concentration (H2) was surveyed on March 25 at an altitude of 30.5 m to allow for the classification of pup developmental stages (see below). The survey strip width was 200 m (100 m per observer) and transects were spaced at intervals of 3.7 km.

Photographic surveys

Fixed-wing aerial photographic surveys were flown in a Piper Navajo airplane using a 23 × 23 cm format metric mapping camera (Zeiss RMK/A) equipped with a 150-mm Sonnar lens and Kodak Double-X (2405) aerographic black and white film. All surveys were flown at an altitude of 305 m providing coverage of a 455.5 × 455.5 m area per photo. There was no overlap between consecutive frames. Correct altitude and transect spacing were maintained using a radar altimeter and LORAN C.

To allow us to correct for errors in reading the photographs, images were also obtained simultaneously using a Vinten 70-mm aerial reconnaissance camera fitted with a 76.2-mm quartz lens, a Wratten 18A ultraviolet filter, and Kodak Tri-X (2403) black and white aerographic film. This system recorded images in ultraviolet wavelengths (300–400 nm) and covered an area of ice 228.6 × 228.6 m per frame.

The survey area consisted of two strata: (1) whelping concentrations and (2) scattered pups outside the whelping concentrations. Although we were unable to survey the first whelping concentration, a photographic survey consisting of six east–west transects spaced 7.4 km apart was carried out on the second whelping concentration (H2) on March 25, 1990. The number of pups born outside the main concentrations (Stratum 2) was estimated from photographs taken during a series of low-density coverage surveys in which systematic transects spaced 37 km apart were flown from 54°N to 50°20′N between March 13 and 28.

Photographic counts

Positive prints were examined by a single reader with previous experience identifying seals on photographs obtained from both camera types. Each frame was examined twice using a luminated hand-lens (7–8× magnification) and the positions and number of all seals were recorded on a clear acetate sheet laid over each print.

To develop a correction factor for pups missed or incorrectly identified by the reader, a series of black and white (Zeiss) and ultraviolet (Vinten) photographs taken at the same time were matched to identify identical areas. Seals were identified independently on both images and compared to determine a "best estimate" of the number of pups present (x) which was then regressed on the original Zeiss counts (y), $x = a + by$. The regressions were not constrained to pass through the origin. Separate regressions were derived for transects flown over the whelping concentration and for surveys outside the whelping concentrations flown on March 20 (Table 1). There were few pups on the photographs taken on March 13, so a regression line based on all data was used to correct the counts. Bootstrap estimates (Efron 1981) of the measurement error associated with variation about the regression were calculated based on 200 bootstrap samples for each transect. The measurement error variances of the transects were added to estimate the total measurement error for the survey and added to the sampling variance.

Survey analysis

All surveys were based on a systematic sampling design with a single random start and a sampling unit of a transect of variable length. If transect spacing changed within the survey area, each area of homogeneous transect spacing was treated as a separate survey. The data were analyzed using the methods outlined in Hammill et al. (1992) and Stenson et al. (1993) as summarized here.

The estimated number of pups for the ith survey is given by

$$\hat{N}_i = k_i \sum_{j=1}^{J_i} x_j$$

where J_i = the number of transects in the ith survey, k_i = weighting factor for the ith survey determined by dividing the transect interval by the transect width, and x_j = the number of pups on the jth transect.

© 1997 NRC Canada

For photographic surveys where frames did not overlap:

$$x_j = \frac{l_j \sum_{z=1}^{f_j} t_{jz}}{f_j p_j}$$

where f_j = the number of photographs on transect line j, t_{jz} = the number of seals in the zth frame on the jth transect, l_j = the total transect length, and p_j = the frame length.

This assumes that the distribution and density of pups on the unobserved portions were similar to those in the observed portions. The additional component of error that arises from this assumption was judged to be small and is included in the between-transect variability.

The estimates of error variance were based on serial difference between transects (Cochran 1977, p. 225; Kingsley et al. 1985) and calculated as

$$V_i = \frac{k_i(k_i-1)J_i}{2(J_i-1)} \sum_{j=1}^{J_i-1}(x_j - x_{j+1})^2.$$

A monotonic trend in abundance was observed among the transects flown on March 13. Therefore, the procedure for estimating the variance of the estimator for a systematic sample with a linear trend (Cochran 1977; Kingsley and Smith 1981) was employed:

$$V_i = \frac{k_i(k_i-1)J_i}{6(J_i-2)} \sum_{j=1}^{J_i-1}(x_j - 2(x_{j+1}) + x_{j+2})^2.$$

The total population was estimated as $\hat{N} = \sum_{i=1}^{I} N_i$ and its error variance $\hat{V} = \sum_{i=1}^{I} V_i$ where I is the number of surveys.

Correction for the temporal distribution of births

The birthing period for hooded seals can take up to several weeks (Bowen et al. 1987), while individual pups are weaned after an extremely short lactation which averages only 4 d (Bowen et al. 1985). Therefore, it is necessary to correct survey estimates for the number of pups which may have left the ice prior to the survey or had not been born. To do this, four observers classified hooded seal pups (bluebacks) into one of three distinct age-dependent developmental stages: newborn/thin, fat, and solitary (Bowen et al. 1987). All observers underwent a training period prior to the start of the surveys to ensure consistent classifications of developmental stages as recommended by Stenson and Myers (1988).

Stage classifications were obtained from the first concentration (H1) on March 21 and 23, while classifications from the second concentration (H2) were obtained on March 25 and 27. On March 21, stage classifications were made by the two observers during a survey flown near ice level (15 m or lower). Ten transects, spaced 4.6 km apart, were flown and all of the pups observed within 300 m of the transect line were classified. Additionally, two observers carrying out surveys to estimate abundance (see above) noted the presence or absence of an attending female for each pup within the survey area. Surveys conducted on March 23, 25, and 27 were flown at an altitude of 30.5 m with transect intervals of 3.7 km. All pups within a 50-m strip on either side of the helicopter were classified according to developmental stage. On March 25, stage classifications were combined with visual abundance surveys; pups within an inner 50-m strip were classified, while pups in the outer 50-m strip were only counted.

Using information on the proportion of pups in each of these developmental stages and the duration of each stage (Bowen et al. 1987; Stenson and Myers 1988; Myers and Bowen 1989; Stenson et al. 1993), we independently corrected the survey results for each whelping concentration for pups which were not present on the ice at the time of the survey. The model output provided an estimate of the fraction of the total pups born that were visible to be photographed on any day.

Developmental stages are denoted by the subscript j, and a pup passes from stage j to $j+1$. We specify stage duration in terms of instantaneous transition intensity functions: $\phi_j(\tau) = \lim_{\Delta\tau \to 0}$ (probability an animal passes from stage j to $j+1$ in the interval $[\tau, \tau+\Delta\tau])/\Delta\tau$) where τ is the time spent in stage j. This specifies the force of transition into stage $j+1$ from stage j, given that the animal has spent time τ in stage j. Note that the transition intensities depend only on the current stage and the time spent in that stage to that point. The rate at which pups enter stage j at time t is denoted by $m_j(t)$ and is given by the recurrence relationship

$$m_j(t) = \int_0^\infty m_{j-1}(t-\tau)\phi_{j-1}(\tau)\, d\tau.$$

If there is no mortality, the total number of pups in stage j that can be observed at time t, $n_j(t)$, is the integral of the rate pups entered stage j time τ ago times the probability that those pups have not entered stage $j+1$:

$$n_j(t) = \int_0^\infty m_j(t-\tau)\left(1 - \int_0^\tau \phi_j(s)\, ds\right) d\tau.$$

These two equations adequately describe Stages 1 (newborn/thin) and 2 (fat). Some Stage 3 (solitary) pups may have entered the water and so the fraction of Stage 3 pups that were not visible was also estimated.

The transition intensity, ϕ_j, of Stages 1, 2, and 3 was assumed to follow a gamma density:

$$\phi_j(t) = \rho_j(\rho_j t)^{\kappa_j - 1} e^{-\rho_j t}/\Gamma(\kappa_j)$$

where κ_j is the shape parameter, ρ_j is the scale parameter, and $\Gamma(\ )$ is the gamma function. These parameters were estimated in Bowen et al. (1987).

Our basic assumption was that the starting date of birthing was estimated from independent data, i.e., from reconnaissance surveys, that Stage 3 lasted 3.5 d, and that pups remained on the ice and thus were visible to be surveyed. This left two parameters to be estimated from the stage duration data: the location and shape of the probability distribution of births over time, $m_1(t)$. The maximum likelihood method described by Myers and Bowen (1989) was used to estimate these model parameters.

The confidence region for the parameters of the birthing distribution were based on the likelihood ratio test (Cox and Hinkley 1974, p. 343). That is, if p parameters were fitted to the model, then the parameters that fell within the $100(1-\alpha)\%$ confidence region were those with log likelihood values that were no less than the maximum log likehood minus $\frac{1}{2}\chi^2_{p,\alpha}$. The confidence limits for the derived parameter, i.e., the proportion visible on the day of the survey, were the minimum and maximum within the confidence region.

In order to test the robustness of the estimates and confidence limits, the model was run using a variety of assumptions. The date of first pupping, the functional form of the birthing distributions, the duration of the last developmental stage, and the proportion of pups in the last stage which are visible were varied.

Results

Identification of whelping areas

A single hooded seal pup was first observed among a large whelping concentration of harp seals (54°04′N, 54°46′W) on March 7, 1990. On March 11, a large number of scattered hooded seals were found during fixed-wing reconnaissance transects flown between 51°20′N and 51°40′N and 51°55′W and 54°10′W. A whelping concentration (H1) was located north of this area on March 13 and a satellite transmitter was

© 1997 NRC Canada

deployed southwest of it at 51°53′N, 53°22′W. On March 25, a second whelping concentration (H2) was located slightly north of the first one. Comparision of the locations of the two concentrations after correcting for ice drift estimated from the movements of the satellite transmitter placed near the first (H1) indicated that the two concentrations were independent.

Visual surveys

Visual surveys of both whelping concentrations were successfully completed. The first concentration, located between 51°03′N and 51°31′N and between 50°50′W and 51°42′W, was surveyed on March 21. A total of 4816 pups were counted over 24 transects with a mean density of 10.7 pups/km^2 (SE = 5.7). The number of pups present was estimated to be 26 900 (SE = 1400) (Table 2).

A visual survey of the second concentration was carried out on March 25 and consisted of 18 transects between 51°23′N and 51°57′N and between 50°35′W and 52°08′W. A total of 950 pups were counted for a mean density of 5.3 pups/km^2. A total of 17 600 (SE = 1400) pups were estimated to be present (Table 2).

Photographic surveys

The second whelping concentration (H2) was surveyed photographically on March 25, 1990; a total of 245 pups were counted on 168 photographs obtained along six transects. After correcting for reader errors, pup production was estimated to be 24 500 (SE = 3600) (Table 2). Although larger than the visual survey estimate of the same concentration, the difference is not statistically significant. Combining the two estimates of pup production and weighting by the inverse of the variance results in an estimate of pup production in H2 of 18 500 (SE = 1300) (Table 2).

To estimate of the number of hooded seals giving birth outside the whelping concentrations (Stratum 2), a total of 23 photographic transects were flown on six separate days between March 13 and 28. Based on the flight lines and estimates of drift obtained from the satellite-linked location beacon, transects flown on March 13 and 20 were considered to be independent and were combined to give complete coverage of the survey area. The area to the south of the whelping concentrations, between 51°0′N and 52°0′N and between 51°0′W and 53°56′W, was surveyed on March 13. Although difficulties with the camera resulted in exceptionally low coverage (≤15%), 43 pups were counted on 215 photographs along four transects . The total estimated number of pups present was 22 000 (SE = 10 500) (Table 2).

The six transects flown on March 20 surveyed the area to the north of the whelping concentrations between 52°20′N and 54°0′N and between 52°0′W and 55°0′W. A total of 454 pups were counted on the 339 photographs obtained, resulting in an estimated pup production of 11 500 (SE = 6600) (Table 2).

Correction for temporal distribution of births

Two estimates of the proportion of pups in each stage were available for each of the concentrations (Table 3). The two independent estimates of stage composition of H1 obtained on March 21 were similar; 74% of the pups were estimated to be in Stages 1–3 from the lower altitude (<15 m) transects, while 76.7% were estimated to be in these stages based on data from the higher altitude (92 m) surveys conducted simultaneously.

Table 2. Visual and photographic estimates of hooded seal pup production (thousands) at the Front during March 1990.

	Date	Visual[a]	Photographic	Combined
Concentration				
H1	21	**26.9 (1.4)**		
H2	25	17.6 (1.4)	24.5 (3.6)	**18.5 (1.3)**
Stratum 2	13		**22.0 (10.5)**	
	20		**11.5 (6.6)**	

Note: Surveys included in the final estimate are shown in bold. Standard errors are included in parentheses.

[a]Uncorrected for pups not present on the ice. Corrected estimate for the two concentrations is **49 600 (SE = 2700)**.

An estimated 91% of the pups born in the first whelping concentration (H1) were visible on the day of the March 21 survey. The best fit (maximum likelihood) to the develomental stage classification data obtained from the first whelping concentration (Table 3) was obtained from a model assuming that the birthing distribution followed a log–logistic distribution, that the date of first pupping was March 14, that the length of the last stage was 3.5 d, and that 100% of the last stage were visible. Runs using alternative assumptions concerning the start date, functional form of the birthing distribution, length the last stage is visible, and the proportion of the last stage visible resulted in estimates ranging from 85 to 95%, indicating that the choice of assumptions did not affect the estimate significantly. The standard error on the correction was approximately 4%.

A large proportion of pups were also present during the March 25 surveys of the second whelping concentration (H2). Using a model with the same assumptions but delaying the date of first pupping to March 22 resulted in an estimate of 92% of the pups visible on the day of the survey. The standard error on the correction was again approximately 4%.

The uncorrected estimate of pup production in the two whelping concentrations was 45 400 (SE = 1900) (Table 2). Assuming the most conservative corrections by using the log–logistic distribution (i.e., 91% of the pups were visible in H1 and 92% in H2), the estimate of pup production in these two areas combined corrected for pups which were not present on the ice is 49 600 (SE = 2700). No data were available to allow us to correct for pups not visible during the surveys of pups born outside the whelping concentrations.

Discussion

Although aerial surveys provide a reasonable method of estimating pup production in species such as the hooded seal which are found at relatively low densities over a large, unstable habitat, the accuracy of the estimate obtained is dependent on the degree to which the possible sources of error are minimized. Myers and Bowen (1989) assessed the relative importance of different sources of bias in estimating abundance from aerial surveys of seals and concluded that the greatest source of bias arose from missing whelping concentrations. We believe that the extensive reconnissance con-

© 1997 NRC Canada

Table 3. Summary of pup developmental stage classifications (described in Bowen eta l. 1987) obtained from visual surveys of the whelping concentrations at the Front, 1990.

Date	No. of transects	Stage 1		Stage 2		Stage 3		Total pups
		N	%	*N*	%	*N*	%	
H1								
March 21	10	130	37.0	130	37.0	91	25.9	351
March 23	11	41	5.9	235	33.6	426	60.6	702
H2								
March 25	18	92	19.0	328	67.9	63	13.0	483
March 27	24	23	5.8	220	56.0	150	38.2	393

Note: Stage 1 = newborn/thin bluebacks; Stage 2 = fat bluebacks; Stage 3 = solitary bluebacks.

ducted prior to and during the survey period reduced the likelihood of missing major whelping concentrations.

The second most important source of error is the potential of missidentifying pups on the photographs. The use of two camera systems operating simultaneously allowed us to compare two images obtained at different wavelengths (ultraviolet versus visible) in order to correct for errors which may have occurred during the readings of the photographs. Although it is possible that pups could be missed (or misidentified) on both film types, the count based on matched frames used for the reader error corrections provided the best estimate of the actual numbers present. Overall, the corrections applied were small, indicating that missidentifying pups is not a major problem when surveying hooded seals. This is to be expected considering the contrast between the dark back of the pup and the ice; the errors which were identified usually occurred when the pups were on their backs and only their white undersides could be seen. Previous photographic surveys (Bowen et al. 1987; Hay et al. 1985) did not correct their estimates for errors in reading, but given the results of this study, the corrections would likely have been small. Also, the earlier surveys were flown at lower altitudes, resulting in larger image sizes which likely reduce the number of misidentifications.

The use of the low photographic coverage of the entire area (Stratum 2) was designed to estimate the number of pups born outside the whelping concentrations. The large variances associated with this survey reflect the low level of coverage, the limited number of transects flown on a single day, and the clumped distribution of hooded seals. In contrast with Bowen et al. (1987) who used a similar survey design to estimate hooded seal pup production at the Front in 1984, we found that a greater proportion of the total births occur outside the whelping concentrations (43 versus 17%). Also, the densities of pups observed in the two concentrations 10.7 and 5.3 pups/km^2) were lower than reported in 1984 (56 pups/km^2). The strong winds and extensive ice drifting which occurred in 1990 may have resulted in more diffuse whelping which would account for these differences.

A greater precentage of pups were present on the ice during the surveys in this study (>90%) than in 1984 when only 64% of the pups were estimated to have been present (Bowen et al. 1987). The high proportion we estimated was not affected by alternative model assumptions. The reason for this difference is not clear, but one possibility may be the way in which the model was applied in the two studies. In 1984, one whelping concentration was located and a single unimodal curve fitted. In 1990, however, two concentrations were identified and separate curves fitted to each one, resulting in two distinct pulses of births. Bowen et al. (1987) noted that the large residuals in their model fitted to the number of pups in the early stages may have been due to a pulse of births between successive surveys which would have been masked by their assumption of a unimodal distribution. Alternatively, the difference in pups present may represent a real change in the shape of the pupping distribution between the two years, pupping being spread over a longer time period in 1984 compared with two distinct pulses in 1990. A change in the temporal distribution of births between 1990 and earlier surveys was observed in harp seals in this area (Stenson et al. 1993), although the reason for such a change is unkown. Such differences among surveys illustrate the variability which may occur and emphasize the importance of estimating pup production outside the whelping concentrations and the temporal distribution of births during each survey.

Population trends

Combining the estimates for the whelping concentrations, corrected for pups which were not present at the time of the survey (49 600 SE = 2700) with the photographic estimates of pups born outside the whelping concentrations on March 13 and 20 (33 500, SE = 12 500), results in an estimate for total pup production of hooded seals at the Front in 1990 of 83 100 (SE = 12 700). Several estimates of pup production at the Front over the past three decades are available (Table 4), although many of these results were obtained using different methods and are not directly comparable. Using the survival index method, pup production from 1966 to 1977 was estimated to be 25 000 – 32 000 (Øritsland and Benjaminsen 1975; Sergeant 1976; Lett 1977; Winters and Bergfløt 1978). These estimates are similar, since they rely on similar data and are heavily influenced by a single high harvest in 1966 (Bowen et al. 1987). A sequential population analysis (Winters and Bergfløt 1978) resulted in a similar estimate for this period but should not be viewed as independent, since the model was fit to an estimate of 1971 pup production obtained from the survival index. Hay and Wakeham (1983) estimated annual pup production between 8000 and 16 000 for the period 1977 – 1982 using a Leslie analysis, but felt that it was likely an underestimate because it only

© 1997 NRC Canada

Table 4. Published estimates of hooded seal pup production (thousands) in the Front, 1963–1990.

Year(s)	Estimate	Confidence interval	Method[a]	Reference
1961–1971	32.8	—	SI	Lett 1977
1963–1978	24–30	—	SPA	Winters and Bergfløydt 1978[c]
1966–1970	31.4	—	SI	Øritsland and Benjaminsen 1975
1966–1971	27.0	—	SI	Sergeant 1976
	27.1	—	SI	Winters and Bergfløydt 1978
1977	11.0	—	Leslie[d]	Hay and Wakeham 1983
1978	13.6	—	Leslie[d]	Hay and Wakeham 1983
1979	16.2	—	Leslie[d]	Hay and Wakeham 1983
1980	12.2	—	Leslie[d]	Hay and Wakeham 1983
1981	9.6[e]	—	Leslie[d]	Hay and Wakeham 1983
1982	7.7	—	Leslie[d]	Hay and Wakeham 1983
1984[b]	62.4	43.7–89.4	AC/VS	Bowen et al. 1987
1985	61.4	16.5–119.5	AC	Hay et al. 1985
1990[b]	83.1	58.2–108[f]	AC/VS	This study

[a]SI, survival Indices; SPA, sequential population analysis; AC, photographic aerial survey; VS, visual survey.

[b]Corrected for pups not present on the ice at the time of the survey.

[c]Tuned to the SI estimate of 27 000 in 1971; assumed mortality rates of 0.135.

[d]Projected mean daily catch rates against cumulative catch. Least squares linear regression used to estimate pup production. Landsmen's catch and catch outside the whelping patches added.

[e]Catch was 10 736.

[f]Approximate 95% CI based on 2 SE.

included whelping concentrations where hunting occurred. There was no estimate of pup production outside these areas or of pups which may have left the ice prior to the time of the hunt.

Aerial photographic surveys were carried out in 1984 and 1985 to estimate pup production at the Front. The survey design used in 1984 was almost identical to the one used in this study, and after correcting for pups born outside the whelping concentration and the temporal distribution of births, Bowen et al. (1987) estimated pup production to be 62 400 (95% CI 43 700 – 89 400). They concluded that the hooded seal population at the Front had likely increased between the 1960's and 1984, although the estimation methods used were different. A photographic survey was also carried out in 1985 (Hay et al. 1985), and although the results (61 400 95% CI 16 500 – 119 450) were similar to those of Bowen et al. (1987), the survey design was slightly different from those used in 1984 and 1990 and the results were not corrected for the temporal distribution of births. Therefore, the only estimate of pup production in hooded seals which can be compared directly with the current study is from the survey conducted in 1984 (Bowen et al. 1987).

Comparing the results of the present study (83 100 SE = 12 700) with those of Bowen et al. (1987) suggests that pup production may have increased slowly (5% per annum) since 1984. However, because of the size of the confidence intervals and the possibility of exchange between the Front and Davis Strait whelping concentration which was not surveyed in 1990, we cannot rule out the possibility of a stable or slightly declining level of pup production. Due to the unavoidable low precision of estimates for this species, more time will be required between surveys to detect any changes which may be occurring and another survey will be necessary before we will be able to determine the rate of change of hooded seal pup production.

Acknowledgements

We would like to thank W. Penney, D. Wakeham, D. McKinnon, J. Brattey, J. Drew, V. Mercer, E. Perry, and our helicopter pilots K. Steele and P. McLelland without whose help the surveys would not have been completed. We would also like to thank the crew of the the CCGS *Sir John Franklin* for their invaluable assistance, the aircraft pilots and crew for their dedication, D. Wakeham for reading the photographs, and M. Hammill, M. Kingsley, D. Bowen, and W. Stobo for assistance in planning the study. We also thank E. Perry, J. Lawson, and B. Sjare who reviewed earlier versions of this manuscript and two anonymous reviewers whose comments improved this manuscript greatly. Support for this work was provided under the Government of Canada's Atlantic Fisheries Adjustment Program (Northern Cod Science Program).

References

Anonymous. 1995. Report of the Joint ICES/NAFO Working Group on Harp and Hooded Seals. North Atl. Fish. Org. SCR Doc. 95/16, Ser. No. N2569.

© 1997 NRC Canada

Bishop, C.A., Anderson, J., Dalley, E., Davis, M.B., Murphy, E.F., Rose, G.A., Stansbury, D.E., Taggart, C., and Winters, G. 1994. An assessment of the cod stock in NAFO Divisions 2J+3KL. North Atl. Fish. Org. SCR Doc. 94/40, Ser. No. N2410.

Bowen, W.D., Oftedal, O.T., and Bowness, D.J. 1985. Birth to weaning in 4 days: remarkable growth in the hooded seal (*Cystophora cristata*). Can. J. Zool. **63**: 2841–2846.

Bowen, W.D., Myers, R.A., and Hay, K. 1987. Abundance estimation of a dispersed, dynamic population: hooded seals (*Cystophora cristata*) in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **44**: 282–295.

Bowering, W.R., Brodie, W.B., and Power, D. 1994. Greenland halibut in NAFO Subarea 2 and Divisions 3KLM: a rapidly declining resource with a rapidly increasing fishery. North Atl. Fish. Org. SCR Doc. 94/57, Ser. No. N2428.

Cochran, W.G. 1977. Sampling techniques. 3rd ed. John Wiley & Sons, London.

Cox, D.R., and Hinkley, D.V. 1974. Theoretical statistics. Chapman and Hall, London.

Efron, B. 1981. Non parametric standard errors and confidence intervals. Can. J. Stat. **9**: 139–172.

Hammill, M.O., Stenson, G.B., and Myers, R.A. 1992. Hooded seal (*Cystophora cristata*) pup production in the Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **49**: 2546–2550.

Hay, K., and Wakeham, D. 1983. Use of catch and effort data to estimate the pup production of hooded seals (*Cystophora cristata*) at Newfoundland. North Atl. Fish. Org. SCR Doc. 83/85, Ser. No. N709.

Hay, K., Stenson, G.B., Wakeham, D., and Myers, R.A. 1985. Estimation of pup production of hooded seal (*Cystophora cristata*) at Newfoundland during March 1985. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 85/96.

Kingsley, M.C.S., and Smith, G.E.J. 1981. Analysis of data arising from systematic transect surveys. *In*: Proc. Symp. Census and Inventory Methods for Populations and Habitats, Banff, April 1980. *Edited by* F.L. Miller and A. Gunn. Contribution No. 217, Forest, Wildlife and Range Experiment Station, University of Idaho, Moscow, Idaho. pp. 40–48.

Kingsley, M.C.S., Stirling, I., and Calvert, W. 1985. The distribution and abundance of seals in the Canadian High Arctic, 1980–1982. Can. J. Fish. Aquat. Sci. **42**: 1189–1210.

Lawson, J.W., Stenson, G.B., and McKinnon, D.G. 1994. Diet of harp seals (*Phoca groenlandica*) in 2J3KL during 1991–93. NAFO Sci. Counc. Stud. **21**: 143–154.

Lett, P.F. 1977. A model to determine stock size and management options for the Newfoundland hooded seal stock. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 77/25.

Morgan, M.J., Bowering, W.R., and Brodie, W.B. 1994. A comparison of results from Canadian deepwater surveys in 1991 and 1994, with emphasis on Greenland halibut. North Atl. Fish. Org. SCR Doc. 94/53, Ser. No. N2424.

Myers, R.A., and Bowen, W.D. 1989. Estimating bias in aerial surveys for harp seal pup production. J. Wildl. Manage. **53**: 361–372.

Øritsland, T., and Benjaminsen, T. 1975. Additional data on the sex ratio, age composition and mortality of Newfoundland hooded seals, with an estimate of pup production and sustainable yield. Int. Comm. Northwest Atl. Fish. Res. Doc. 75/122.

Power, D. 1994. The status of Divisions 3LN redfish resource. North Atl. Fish. Org. SCR Doc. 94/54, Ser. No. 2425.

Ross, S.-A. 1992. Food and feeding of the hooded seals *Cystophora cristata* in Newfoundland. M.Sc. thesis, Memorial University of Newfoundland, St. John's, Nfld.

Sergeant, D.E. 1976. Research on hooded seals *Cystophora cristata* Erxleben in 1976. Int. Comm. Northwest Atl. Fish. Res. Doc. 76/X/126.

Sinclair, A. 1993. Report on the assessments of groundfish stocks in the Canadian Northwest Atlantic, May 4–14, 1993. Can. Tech. Rep. Fish. Aquat. Sci. No. 1946e.

Stenson, G.B., and Kavanagh, D.J. 1994. Distribution of harp and hooded seals in offshore waters of Newfoundland. NAFO Sci. Counc. Stud. **21**: 121–142.

Stenson, G.B., and Myers, R.A. 1988. Accuracy of pup classifications and its effect on population estimates in the hooded seals (*Cystophora cristata*). Can. J. Fish. Aquat. Sci. **45**: 715–719.

Stenson, G.B., Ni, I-H., Ross, S.-A., and McKinnon, D. 1991. Hooded seal, *Cystophora cristata*, feeding and interactions with commercial fisheries in Newfoundland. Can. Atl. Fish. Sci. Adv. Counc. Res. Doc. 91/45.

Stenson, G.B., Myers, R.A., Hammill, M.O., Ni, I-H., Warren, W.G., and Kingsley, M.C.S. 1993. Pup production of harp seals, *Phoca groenlandica*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2429–2439.

Winters, G.H., and Bergfløedt, B. 1978. Mortality and productivity of the Newfoundland hooded seal stock. Int. Comm. Northwest Atl. Fish. Res. Doc. 78/xi/91.

© 1997 NRC Canada

An observation on the reaction of Atlantic cod (*Gadus morhua*) in a spawning shoal to bottom trawling

M.J. Morgan, E.M. DeBlois, and G.A. Rose

Abstract: The reactions of Atlantic cod (*Gadus morhua*) in spawning condition to a single pass with an otter trawl were observed by repeatedly transecting the trawl track through a cod shoal with a 38-kHz echosounding system. The shoal consisted of a 5-km-wide band of fish extending approximately 25 km along the 390-m isobath and occupying the bottom 10 m at varying densities averaging 0.004 fish·m^{-3} (maximum 0.488·m^{-3}). The shoal comprised cod of a mean size of 41 ± 6.1 cm. Following passage of the trawl, a 300-m-wide "hole" in the aggregation spanned the trawl track. Disturbance was detected for 77 min after passage of the trawl. Densities were very low in and near the trawl track and increased up to a distance of 200–400 m on each side of the track (a total distance of 400–800 m). This study is the first to observe large-scale changes in the structure of a shoal of cod in spawning condition, attributable to otter trawling, and indicates that such responses can result in persistent disturbances within the shoal over relatively large distances.

Résumé : Pour observer les réactions de morues franches (*Gadus morhua*) en période de fraye à un seul passage d'un chalut à panneaux, nous avons à plusieurs reprises coupé le sillage du chalut avec un sondeur acoustique de 38 kHz à travers un banc de morues. Le banc était formé d'une mouvée de poissons de 5 km de large, s'étendant sur environ 25 km le long de l'isobathe de 390 m, et occupant une zone de 10 m au-dessus du fond, à des densités variables dont la moyenne se situait à 0,004 poisson·m^{-3} (valeur maximale 0,488 poisson·m^{-3}). Le banc était formé de morues dont la taille moyenne était de 41 ± 6,1 cm. À la suite du passage du chalut, un « trou » de 300 m de largeur s'est formé dans le groupe de poissons tout au long du sillage laissé par le chalut. Des perturbations ont été détectées pendant 77 min après le passage du chalut. Les densités étaient très basses dans le sillage du chalut et à proximité de celui-ci, et augmentaient sur une distance de 200 à 400 m de chaque côté du sillage (soit une distance totale de 400 à 800 m). Cette étude est la première à rendre compte de changements à grande échelle dans la structure d'un banc de morues en période de fraye, changements qui peuvent être attribués à l'utilisation d'un chalut à panneaux; elle indique que pareilles réactions de la part des poissons peuvent causer des perturbations persistantes au sein du banc sur des distances relativement importantes.
[Traduit par la Rédaction]

Introduction

Fishes derive many benefits from shoaling. These include increased foraging efficiency, decreased risk of predation, increased accuracy of migration, and benefits from reproductive synchrony (Pitcher 1986). Atlantic cod (*Gadus morhua*), like many commercial species, spend much of their time in shoals. They form large groups prior to spawning, which they maintain throughout the spawning period (Brawn 1961). In Newfoundland waters, cod migrate after spawning, again in large shoals, to inshore feeding areas (Rose 1993).

These large shoals, particularly the prespawning and spawning shoals, have been the target of the commercial otter trawl fishery since the 1960's. Despite the importance of this fishery and its prosecution during the prespawning and spawning period, no research has been conducted on the impact of trawling on the behavior of cod in these groups.

Direct observations using divers and underwater cameras have shown that, in general, fish in shoals react to an otter trawl by turning away from the approaching doors. Some fish turn into the trawl and are caught, while others turn away from the trawl and escape (Wardle 1986). However, the reaction of fish beyond the immediate vicinity of the trawl and the extent and degree of disruption of the shoal have not been addressed.

The potential influence of fishing on reproductive and migratory behaviors has also received little attention. There is some evidence that fish in spawning shoals may be less responsive to trawls than nonspawning fish. For instance, Atlantic herring (*Clupea harengus*) in spawning schools show very little response to a midwater trawl, while nonspawning herring move away from the fishing gear (Mohr 1964). It is not known how cod in spawning condition would react to the passage of a trawl. Cod are considered to be a nonobligate schooling species (Harden-Jones 1968) whose aggregative nature and specific behaviors are greatly influenced by their reproductive and migratory cycles (Rose

Received January 31, 1995. Accepted August 6, 1995.
J13231

M.J. Morgan and G.A. Rose.[1] Department of Fisheries and Oceans, P.O. Box 5667, St. John's, NF A1C 5X1, Canada.
E.M. DeBlois. DeBlois & Associates, 5 Middle Battery Rd., St. John's, NF A1A 1A2, Canada.

[1] Present address: Fisheries and Marine Institute, Memorial University of Newfoundland, St. John's, NF A1C 5R3, Canada.

© 1997 NRC Canada

1993). The structure of cod spawning shoals is almost certainly related to spawning behavior. There is pair formation and courtship behavior with spawning occurring with the pair in close physical contact. There is also aggression between males that results in spacing between reproductively active individuals (Brawn 1961). Also, large shoals of spawning cod characterized by relatively constant and elevated densities and common structural patterns have been observed with echosounders off Norway (Sund 1935) and Newfoundland (Rose 1993). The internal structure of spawning cod shoals could be disrupted by trawling. Such disruptions could have a negative impact on spawning if time and energy are wasted in reestablishing shoal structure.

In this study, we describe the reaction of cod in a spawning shoal in Newfoundland waters to an otter trawl.

Materials and methods

The study took place on the northern Grand Banks near 49°41′N, 49°51′W on May 25, 1992, in 400 m of water (Fig. 1), an area where cod are thought to spawn (Hutchings et al. 1993) and where large catches are taken during this time of year in research vessel surveys (Bishop et al. 1994).

Two vessels were used, one equipped for scientific echosounding and the other for bottom trawling. Acoustics were conducted from a 60-m vessel (RV *Lady Hammond*) equipped with a 38-kHz dual beam echosounder, transmitting a 0.4-ms pulse each second (Biosonics, Inc., model 102) and linked with a Global Positioning navigation system (GPS). The transducer (6–16°) was housed in a 1.5-m V-fin towed amidships at a depth of 60 m at 3.5 kn. The acoustic system was calibrated with a standard reference sphere both before and after the experiment (Rose and Porter 1996). Acoustic signal levels and GPS latitude and longitude were stored in digital format. Cod densities were derived for surface-referenced blocks with approximate dimensions of 10 m depth × 100 m horizontal for general shoal description and 1 × 10 m for the experiment using standard integration techniques (MacLennan and Simmonds 1992). In addition to the surface-referenced integration blocks, simultaneous integration was conducted in the bottom 10 m over 0.5-m strata referenced to the bottom. Bottom signal was removed from the surface-referenced density estimates by a sequential bottom-up subtraction procedure based on the observed inflection point in the bottom-referenced integrated values (Biosonics, Inc. 1990). We assume that losses within the acoustic "dead zone" (MacLennan and Simmonds 1992) are equivalent across the transects. Integrated densities were scaled to absolute values employing an empirically determined target strength value (–34 dB·fish^{-1}) determined from ex and in situ experiments (Rose and Porter 1996).

Fishing was conducted from the RV *Alfred Needler*, a 50-m stern trawler. A two-bridle Western IIA box otter trawl, equipped with bobbin gear and 950-kg (4-m^2) slotted cambered doors, was towed at a speed of 3.5 kn (see Carrothers 1988 for trawl specifications). Fish caught were sampled for length, sex, and maturity according to the scheme of Templeman et al. (1978).

The experiment began with the location of a relatively large shoal of cod (Fig. 1). The acoustic record indicated that the shoal contained spawning activity (Rose 1993), which was later confirmed by sampling of the fish. The shoal was then crossed to map its dimensions and determine its base structure in an untrawled state. After the shoal was mapped acoustically, a baseline acoustic transect was conducted and an experimental trawl transect was chosen that bisected the shoal. Although the GPS-determined coordinates of the transect were used by the navigators of each vessel, visual contact was used to improve the synchronicity of the vessels. The acoustic vessel led the trawler through the transect and then turned to cut across the trawl line directly behind the trawler.

Four trials over a period of 48 h were attempted but only one was successful in synchronizing both vessel tracks. The other attempts were each rejected for a separate reason. In one, there was too much noise in the acoustic data, in another the trawler did not catch any fish, and in the last the position of the trawl given by the trawler's navigation system did not match the position of the transects from the acoustic vessel's navigation system. The successful trial consisted of a baseline transect of 2.4 km, a fishing tow lasting 28 min, and four transects across the trawl path following trawling (Fig. 1). The fishing tow began at 20:16 NDT which was near dusk. The first transect began at 20:30 NDT and the last ended at 21:41 NDT, well after dark.

For each acoustic transect, before and after trawling, the average and maximum density of fish in the shoal was calculated. Shoal structure was summarized using a surface mapping software (Surfer version 5.01). Plots generated provided a clear representation of the vertical and horizontal distribution of fish within the shoal.

Results

The cod shoal was distributed along the 390-m isobath of the North Cape of the Grand Bank at a depth range of 375–420 m (Fig. 1). It consisted of a 5-km-wide band of fish which extended over a distance of 25 km. Before trawling, the shoal was characterized by discrete edges but did not exhibit a fully homogeneous structure (Fig. 2). Within-shoal densities measured at fine resolution (10 × 10 m) varied over at least 2 orders of magnitude (0.004 ± 0.014, mean ± SD, maximum 0.488 fish·m^{-3}). The vertical structure of the shoal was irregular, with peaks and troughs and several columnar structures and small groups above the main body of fish. However, over the entire aggregation, most fish occurred within the bottom 10 m.

A total of 484 cod were caught by the trawl during the single fishing tow, 198 males and 286 females. The average length of the fish was 41.1 cm (±6.1 cm). Forty-three percent of the cod were mature, and of those, 14.4% were in spawning condition. This indicated that some spawning was occurring in this shoal. This mixture of immature fish and mature fish in various stages of spawning is typical of shoals of cod during the spawning season (M.J. Morgan, unpublished data).

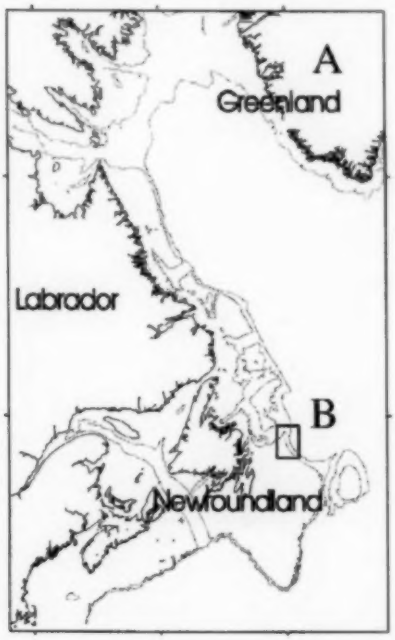
After trawling, the path of the trawl was clearly visible in the acoustic record of all transects (Fig. 2). Transect 1 was 2 km long and took place from 6 to 19 min after the trawl had passed. The trawl path was centered near the 1-km mark. Fish displacement was clearly visible in the density plot around the trawl path and extended over an area of 300 m. Shoal height off the bottom was lowest in this "hole" (2 m) and greatest on either side of the trawl path where the fish extended to 13 m from the bottom. The mean density across this transect was 0.0044 ± 0.014 fish·m^{-3} with a maximum density of 0.2776 fish·m^{-3}.

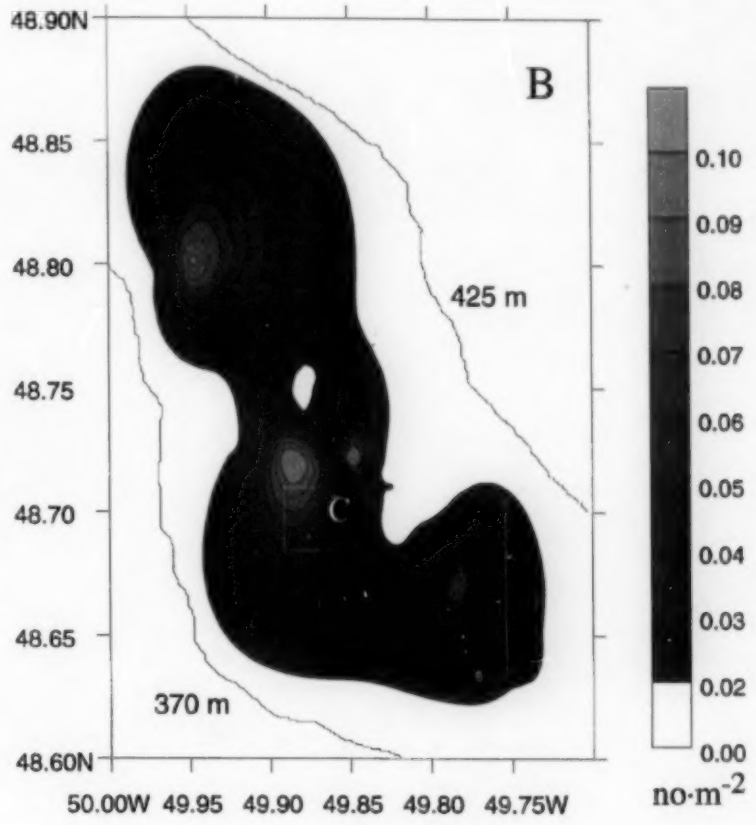
Transect 2 was 1.8 km long and took place from 22 to 34 min following the passage of the trawl. The trawl path, centered at about the 750-m mark, was not as distinct as in transect 1 (Fig. 2). But, as in the first transect, the shoal extended farthest from the bottom on either side of the trawl path. The mean density of fish in the shoal was 0.0050 ± 0.016 fish·m^{-3} with a maximum density of 0.3127 fish·m^{-3}.

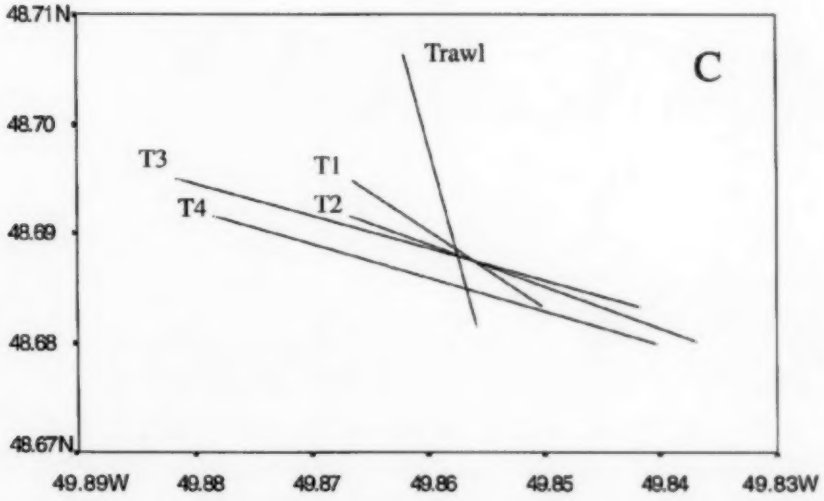
Transect 3 took place from 36 to 57 min after trawling and was 3 km long. Effects of trawling were evident over a 150- to 200-m-wide area at the 1550-m mark (Fig. 2). Again the shoal reached its greatest extension from the bottom (17 m)

© 1997 NRC Canada

Fig. 1. Sampling location and experimental design. (A) Northeast Newfoundland Shelf with the survey area located in the box. (B) Areal contours of the cod shoal on May 25, 1992, prior to the experiment. Densities in fish·m^{-2} are integrated over each 100 m. Maximum densities are approximately 20 fish·m^{-2}. Contours were generated by normal kriging. The experimental trawl and acoustic transects were located in the area encompassed by the box. (C) Location of trawl and transects across the trawl path. T1–T4 are the acoustic transects.

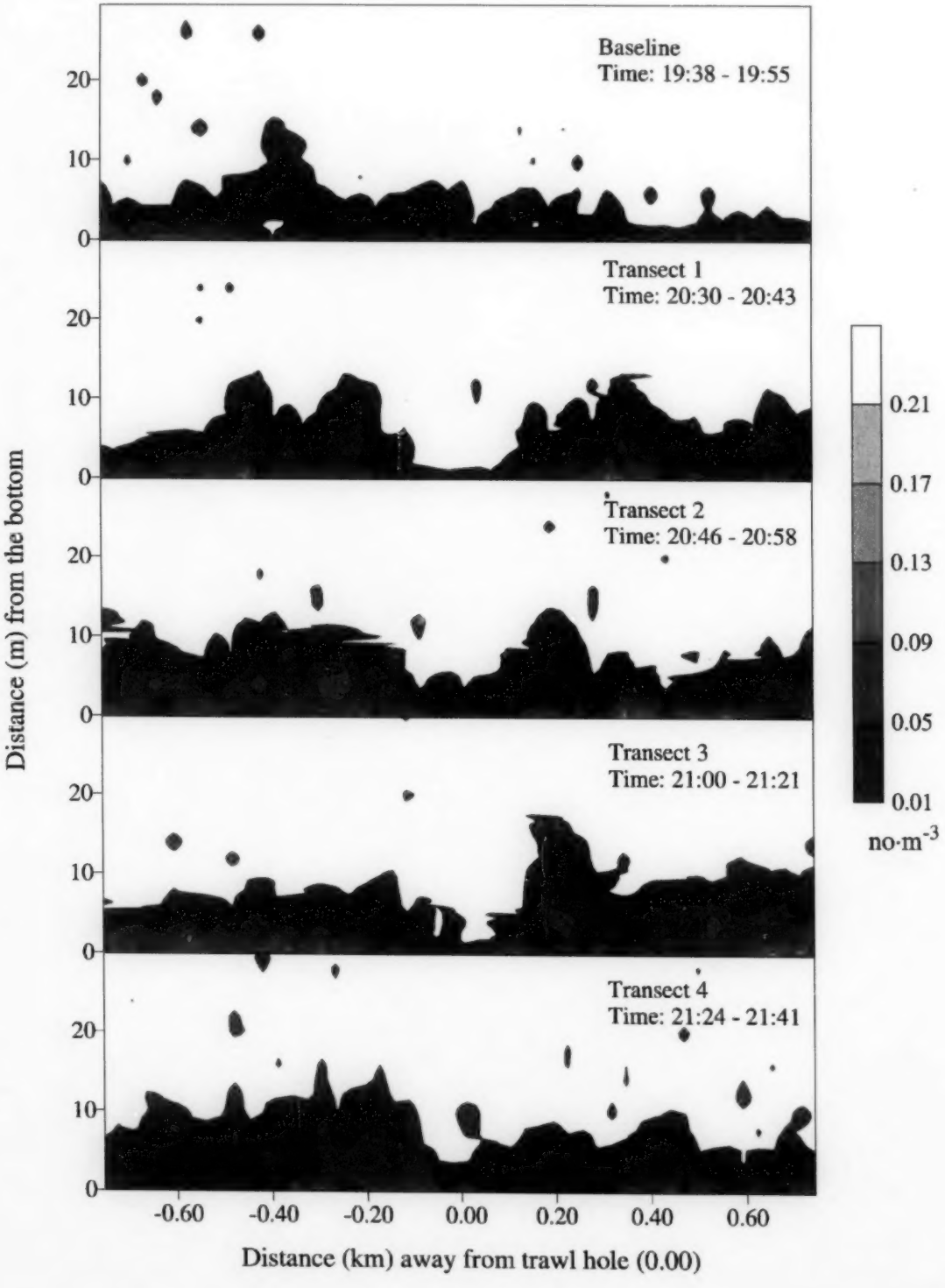






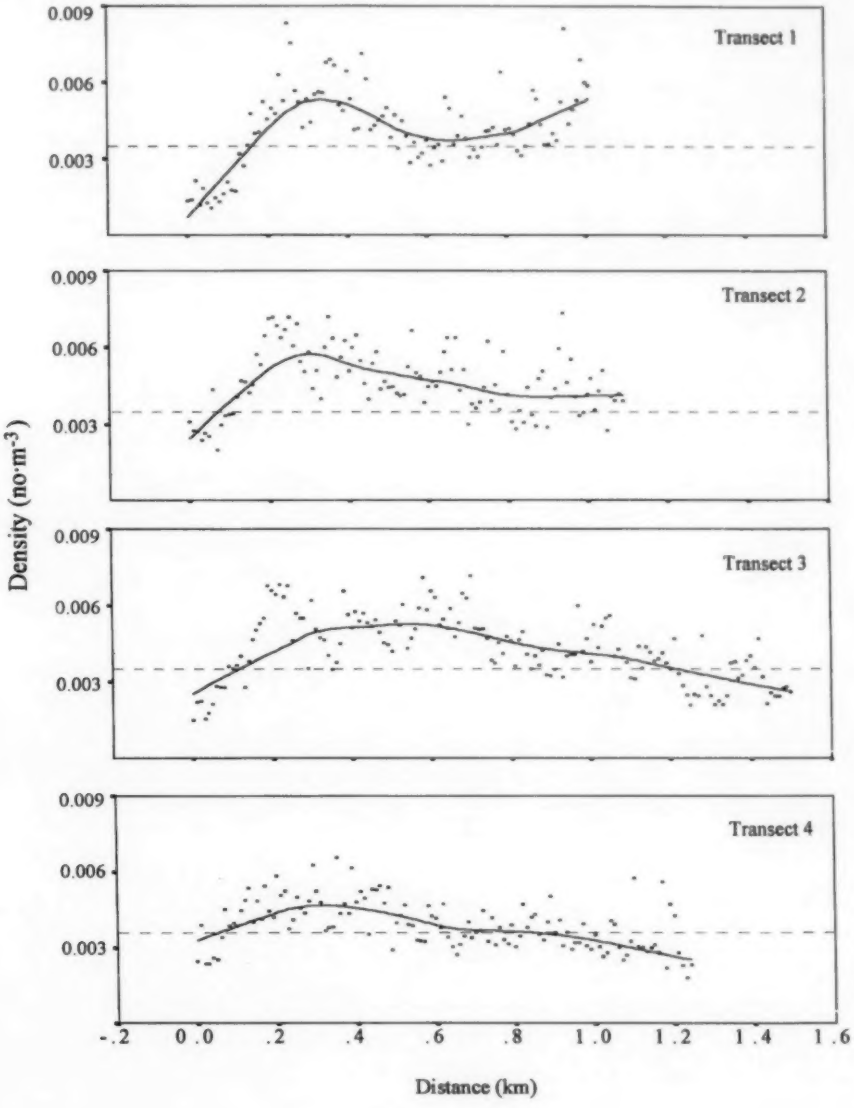
© 1997 NRC Canada

Fig. 2. Density of cod along the acoustic transects. Contours were generated by normal kriging. The baseline transect was conducted before trawling occurred. Transects 1–4 were those conducted across the trawl path and are standardized so that the zero position is the path of the trawl.



© 1997 NRC Canada

Fig. 3. Depth-averaged densities with increasing distance from the trawl path for all acoustic transects that were conducted after trawling. The zero position on the horizontal axis is the center of the trawl path. A Lowess smoother (solid line) has been applied to the data for each transect to illustrate the trends. The broken horizontal line is the average pretrawl density.



next to the trawl "hole" at about the 1750-m mark. The maximum density of fish was 0.3037 fish·m^{-3} with an average density of 0.0045 ± 0.014 fish·m^{-3}.

The final acoustic transect was conducted from 60 to 77 min after trawling and covered 2.4 km. The transect intersected the trawl path at the 1300-m mark, where a "hole" was still visible. Within the trawl "hole", fish extended to 4 m from the bottom. The mean density across this transect was 0.0041 ± 0.013 fish·m^{-3} with a maximum density of 0.2900 fish·m^{-3} (Fig. 2).

The acoustic density of the cod aggregation after trawling exhibited a consistent pattern relative to the trawl track. In each transect following trawling, depth-averaged density was low within and near the trawl path and then increased with increasing distance from the trawl path (Fig. 3). On average, density increased up to a distance of 200–400 m on each side of the path of the trawl. This indicates that the total area of influence of the trawl extends for a distance of at least 400–800 m across the shoal.

Discussion

Our data suggest that cod in spawning shoals do react to and can avoid the passage of an otter trawl. This reaction affects

© 1997 NRC Canada

the shoal structure up to approximately 200–400 m on either side of the trawl path and lasts up to at least 77 min. The avoidance response results in an increase and then decrease in fish density, with increasing distance from the trawl path. The observations presented here are the first on the extent to which the avoidance reaction of fish to a trawl spreads throughout a shoal.

The reaction observed here is likely to be a response to the trawl rather than to the acoustic vessel. Studies by Ona and Godø (1990) indicate that avoidance of vessel noise is not likely to occur at depths of 400 m. Also, multivessel sequential acoustic experiments on cod and capelin (*Mallotus villosus*) have indicated that vessel avoidance is not an important source of variation in acoustic measures at these depths (G.A. Rose, unpublished data).

The densities measured across the shoal were highly variable, at least in part as a consequence of the high resolution of our observations. This 10-m horizontal scale averages only five to six pings of the echosounder. Substantial ping-to-ping variability in the backscatter from even a single fish as a result of equipment variations and target directionality is well known (Nakken and Olsen 1977). Hence, a portion of the variability in density may be artifact. However, these factors are thought to have a maximum effect of 2–3 dB and would not likely account for the 2 orders of magnitude variation in density observed here. Also, the footprint of the 6° beam spanned an average of 40 m during the transects which should tend to smooth and reduce spurious high-frequency variations. We conclude that the high levels of variability observed were largely not caused by backscatter or equipment variability but by true variation in fish density.

Changes in density that were observed with increasing distance from the trawl did not result solely from fish capture. The door spread of a Western IIA trawl at 400 m is expected to be approximately 65 m (Koeller 1991). Trawl "holes" were approximately 300 m wide, much more than the expected door spread of a Western IIA.

Previous observations have shown that fish react to trawl doors by turning away from them. This results in the fish turning either away from or into the trawl (Wardle 1986). The pattern of changing density observed here suggests that the fish that turn away from the trawl may continue to move away for up to 200–400 m. As the cod move away from the path of the trawl, an increasing number stop their avoidance reaction, resulting in increasing density with increasing distance from the trawl. At the point of highest density (200–400 m), most fish stop their avoidance response. We believe that the observed displacement from the trawl probably reflects a combination of actual response of individual fish to the trawl and to shoal neighbors. Avoidance of an approaching stimulus is known to spread throughout a shoal beyond the immediate reaction zone through the response of individuals to their neighbors (Godin and Morgan 1985). The duration of this response may also be a combination of response to the trawl and to other fish. During the first acoustic transect the fish may have been reacting to the noise of the trawl which was still being towed along the final portion of its path. On this and other transects, there may have been cues resulting from the disturbance of sediment. Also, just as the reaction of fish to their neighbors propagates the response farther into the shoal than the immediate influence of the trawl, this reaction may sustain the response longer than the duration of any direct cues from trawling.

Most previous studies have examined the reaction of fish in the immediate vicinity of the trawl (see Ferno 1993 for a review). Ona and Godø (1990) were able to detect horizontal movements of cod and haddock away from an approaching trawl but could not determine how far these reactions extended. They found that the shoal returned to its pretrawl structure within 6–7 min following the passage of the trawl. The difference in the length of time the reaction was detected may result from differences among species. It might also be because the fish studied by Ona and Godø (1990) were not in spawning condition. The impact of trawl avoidance behavior on spawning cod will depend on the importance of the shoal structure to spawning. If cod in spawning shoals do space themselves by means of aggression as suggested by Brawn (1961), then disruption of this spacing would occur when fish avoid the trawl. Spacing would have to be reestablished within the zone of reaction, in this case 200–400m on either side of the trawl path. Repeated trawling during commercial fishing may alter the reaction of the fish to the trawl (Zaferman and Serebrov 1989). It is possible that the fish would habituate to the repeated trawling and that the reaction to the trawl would be much less extensive. Conversely, repeated avoidance of trawls could heighten the response of the fish, leading to even greater disruption of shoal structure. These questions cannot be answered by this study.

Acknowledgements

This study was supported by the Northern Cod Science Program and the Ocean Production Enhancement Network. We thank the crews of the Vessels *Alfred Needler* and *Lady Hammond* and the technical staff of the Groundfish Division for their cooperation and assistance. C. Bishop, G. Evans, P. He, S. Walsh, and an anonymous reviewer gave helpful comments on an earlier version of the manuscript.

References

Biosonics, Inc. 1990. Echo signal processor operators manual. Biosonics, Inc., Seattle, Wash.

Bishop, C.A., Anderson, J., Dalley, E., Davis, M.B., Murphy, E.F., Rose, G.A., Stansbury, D.E., Taggart, C., and Winters, G. 1994. An assessment of the cod stock in NAFO divisions 2J+3KL. NAFO SCR Doc. 94/40, Ser. No. N2410.

Brawn, V.M. 1961. Reproductive behaviour of the cod (*Gadus callarias* L.). Behaviour, **18**: 177–197.

Carrothers, P.J.G. 1988. Scotia Fundy groundfish survey trawls. Can. Tech. Rep. Fish. Aquat. Sci. No. 1609.

Ferno, A. 1993. Advances in understanding of basic behaviour: consequences for fish capture studies. ICES Mar. Sci. Symp. **196**: 5–11.

Godin, J-G.J., and Morgan, M.J. 1985. Predator avoidance and school size in a cyprinodontid fish, the banded killifish (*Fundulus diaphanus* Lesueur). Behav. Ecol. Sociobiol. **16**: 105–110.

Harden-Jones, F.R. 1968. Fish migration. Edward Arnold Ltd., London.

Hutchings, J.A., Myers, R.A., and Lilly, G.R. 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2457–2467.

Koeller, P.A. 1991. Approaches to improving groundfish survey abundance estimates by controlling the variability of survey

© 1997 NRC Canada

geometry and performance. J. Northwest Atl. Fish. Sci. **11**: 51–58.

MacLennan, D.N., and Simmonds, E.J. 1992. Fisheries acoustics. Chapman and Hall, London.

Mohr, H. 1964. Reaction of herring to fishing gear revealed by echosounding. *In* Modern fishing gear of the world 2. *Edited by* Fishing News International and Fishing News. Fishing News (Books) Ltd., London. pp. 253–257.

Nakken, O., and Olsen, K. 1977. Target strength measurements of fish. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **170**: 52–69.

Ona, E., and Godø, O.R. 1990. Fish reaction to trawling noise: the significance for trawl sampling. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **189**: 159–166.

Pitcher, T.J. 1986. Functions of shoaling behaviour in teleosts. *In* The behaviour of teleost fishes. *Edited by* T.J. Pitcher. Croom Helm, London. pp. 294–337.

Rose, G.A. 1993. Cod spawning on a migration highway in the north-west Atlantic. Nature (Lond.), **336**: 458–461.

Rose, G.A., and Porter, D.R. 1996. Target strength studies on Atlantic cod (*Gadus morhua*) in Newfoundland waters. ICES Mar. Sci. Symp. **53**: 259–265.

Sund, O. 1935. Echosounding in fishery research. Nature (Lond.), **135**: 953.

Templeman, W., Hodder, V.M., and Wells, R. 1978. Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of the southern Grand Bank. ICNAF Res. Bull. **13**: 53–65.

Wardle, C.S. 1986. Fish behaviour and fishing gear. *In* The behaviour of teleost fishes. *Edited by* T.J. Pitcher. Croom Helm, London. pp.463–495.

Zaferman, M.L., and Serebrov, L.I. 1989. On fish injuring when escaping through the trawl mesh. ICES C.M. 1989/B:18.

© 1997 NRC Canada

Inshore exploitation of Newfoundland Atlantic cod (*Gadus morhua*) since 1948 as estimated from mark–recapture data

Ransom A. Myers, Nicholas J. Barrowman, and Jeffrey A. Hutchings

Abstract: We use tagging studies to estimate fishing mortality (F) of inshore populations of Atlantic cod (*Gadus morhua*) around Newfoundland. New methods have been developed for this analysis that allow fishing mortalities and reporting rates to be estimated for different sectors of a fishery, e.g., inshore fixed gear and offshore trawlers. We find that the fishing mortalities on inshore components of the cod stocks have been high since 1948, when the estimated fishing mortality was greater than 0.5. Since then the fishing mortality has increased, and in recent years has been much greater than the population can sustain. There is a critical need to define inshore stocks and to institute conservation measures specific to inshore populations.

Résumé : Nous utilisons des études de marquage afin d'estimer la mortalité par pêche (F) des populations côtières de morue franche (*Gadus morhua*) autour de Terre-Neuve. Pour notre analyse, nous avons développé de nouvelles méthodes qui permettent l'estimation des taux de mortalité par pêche et des taux de déclaration des prises pour les différents secteurs d'une pêche, p.ex., pour la pêche côtière aux engins fixes et pour les chalutiers hauturiers. Nous trouvons que les taux de mortalité par pêche dans les composantes côtières des stocks de morue sont élevés depuis 1948, alors que le taux estimatif de mortalité par pêche était supérieur à 0,5. Depuis ce temps, la mortalité par pêche a augmenté et, dans les dernières années, elle a été de beaucoup supérieure à ce que la population peut supporter. Il est impératif de définir les stocks côtiers et d'instaurer des mesures de conservation visant de façon spécifique les populations des eaux côtières. [Traduit par la Rédaction]

Introduction

Fisheries are often managed under the assumption that breeding populations are large and generally follow the management units that are convenient to administer. However, if a "stock" is actually composed of many independent or semiindependent populations, then it is easy to overexploit or eliminate the subpopulations that are more easily fished (Clark 1990). This is perhaps the most difficult problem in the management of exploited populations. Here we analyze tagging data from 1948 to 1991 to estimate the exploitation of subpopulations of Atlantic cod (*Gadus morhua*) around Newfoundland. We examine inshore stock components because there is strong evidence that they have been historically subject to overexploitation (Templeman 1966; Hutchings and Myers 1994, 1995).

We develop new methods that allow us to separate fishing mortality into different components, e.g., inshore and offshore mortality. Our methods are similar to Brownie "band return" models (Brownie and Pollock 1985; Pollock 1991) in that they do not assume that the commercial catch is known. This is important because we will attempt to estimate the exploitation rate on subpopulations, and it is impossible to obtain commercial catches separated in an appropriate fashion. Pollock et al. (1991) were the first to point out that band return models can be used to apportion exploitation rate among different user groups although we are unaware of any such analysis.

It is clear that the stock structure of cod around Newfoundland is complex. There is evidence of four types of subpopulations: (1) bay stocks, i.e., subpopulations that spawn and overwinter in deep bays such as Trinity Bay and Placentia Bay (Neilsen 1895; Hutchings et al. 1993; Smedbol and Wroblewski 1997), (2) headland stocks, i.e., subpopulations that overwinter in the deep water off headlands such as Cape Bonavista (Templeman 1966), (3) offshore migrants that overwinter on the edge of the continental shelf and migrate inshore to feed in the summer (Lear 1984), and (4) offshore residents that do not migrate inshore (Lear 1984). We examine data on groups of cod that may be a mixture of the first three types of subpopulations, the fourth being excluded because we examine tagging that only occurred inshore.

A simple example

Initially we consider a simple case with a fishery in which exploitation takes place over a short period, e.g., the inshore cod trap fishery in 2J3KL lasts for approximately 3 mo. Let the reporting rate (the probability that a tag on a captured fish is reported) be λ. Let the finite exploitation rate, i.e., the proportion of fish caught, be u, and let the proportion of fish that die naturally or lose their tags each year be v (notation

Received January 27, 1995. Accepted January 17, 1996. J13444

R.A. Myers and N.J. Barrowman. Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St John's, NF A1C 5X1, Canada.
J.A. Hutchings. Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

© 1997 NRC Canada

Table 1. Notation.

Parameter	Definition
s	Subscript: fishing stage (1 = offshore, 2 = inshore)
y	Subscript: year
k	Subscript: tag type (1 = reference tag)
q	Proportion of fish that die immediately from tagging
ρ	Proportion of fish that retain their tags immediately after tagging
$G(t)$	Probability of tag retention at time t, conditional on initial tag retention
$Q(t)$	$= \rho G(t)$; proportion of fish that retain their tags at time t
ϕ_k	Instantaneous rate of tag shedding of tag type k
λ	Reporting rate
θ	$= (1 - q)\rho\lambda$; proportion of tags potentially available to be recovered, namely those that survive the tagging, are initially retained, and will be reported if captured
θ_{sk}	Value of θ for fishing stage s and tag type k
M	Instantaneous natural mortality per year
r_0	Recoveries during the late fall immediately after tagging
v	Finite natural mortality plus tag shedding rate
u_s	Finite exploitation rate for fishing stage s
F_s	Fishing mortality for fishing stage s
r_{syk}	Observed tag returns from fishing stage s in year y of tag type k
r_{s0k}	Observed tag returns from fishing stage s until end of year for fall tag release
t_F	Fraction of year between tagging and the next June
N_k	Number tagged with tag type k
N'_{sk}	$= (N_k\theta_{sk} - r_{s0k})e^{-(M+\phi_k)t_F}$; effective number of fish released for fishing stage s with tags of type k at the start of the first fishing season after tagging

is given in Table 1). Assume that N tags are applied just before the fishing season and that the fishing season is short so that natural mortality and tag shedding can be assumed to occur only between the periods of fishing. If λ, u, and v do not vary over time, then the expected tag returns for the first three years will be as follows:

Year 1	Year 2	Year 3
$Nu\lambda$	$N(1-u)(1-v)u\lambda$	$N(1-u)^2(1-v)^2u\lambda)$

If v is known, then it is possible to estimate u and λ in the above example. For example, dividing the observed number of tag returns in the second year by the number in the first year is an estimate of

$$\frac{N(1-u)(1-v)u\lambda}{Nu\lambda} = (1-u)(1-v)$$

and if v is known, then u can be estimated. The observed number of returns in year 3 can then be equated with the expected number and the equation solved for the remaining unknown, λ. It is simple to write down the likelihood equation for the parameters λ and u given the observed returns and obtain maximum likelihood estimates of the parameters. This formulation is similar to the basic catch equations for tagging data described by Beverton and Holt (1957) and Ricker (1958).

This model is also similar to bird banding return models (Brownie and Pollock 1985; Pollock 1991) in that there is no assumption that the catch is known. The models differ in that in band return models the total survival is usually estimated, while our model concentrates on estimating the exploitation rate with the assumption that natural mortality is known. Another difference in our approach is that we usually have only one year of tagging, while in banding models, tagging is typically carried out for a number of years in the same location. Our exploitation rate, u, is the same as the annual kill probability, K, in band return models, and our λ has the same interpretation as in band return rates.

In most applications of mark–recapture, the tagged animals are assumed to mix through the population. We will not make that assumption here because we are interested in exploitation rates of subpopulations or components of a larger population that cannot easily be identified. Thus, our estimates of exploitation rate will be those for components of the population.

The model used in this paper (Table 2) is an elaboration of the simple model which takes into account tag shedding, returns during the end of the year after tagging, fishing in inshore and offshore sectors, and different tag types. The sections that follow explain these details.

Tag shedding and a correction for the first year

In the above example, we considered natural mortality and tag shedding together in one parameter, v, which was assumed constant. In general, we represent the probability that a fish retains its tag at time t after release as

$$Q(t) = \rho G(t)$$

where $G(t)$ is the probability of tag retention at time t *conditional on initial tag retention*, with $G(0) = 1$, so that $\rho = Q(0)$

© 1997 NRC Canada

Table 2. Expected returns of tag type k for the model used in this paper (for notation, see Table 1).

	Effective number of fish released	×	Probability of capture in year y
Offshore	$(N_k\theta_{1k} - r_{10k})e^{-(M+\phi_k)t_F}$	×	$[(1-u_1)(1-u_2)(1-v_k)]^{y-1}u_1$
Inshore	$(N_k\theta_{2k} - r_{20k})e^{-(M+\phi_k)t_F}$	×	$[(1-u_1)(1-u_2)(1-v_k)]^{y-1}(1-u_1)u_2$

is the probability of initial tag retention. If the instantaneous rate of tag shedding is constant, then $G(t)$ can be expressed as $e^{-\phi t}$, i.e.,

$$Q(t) = \rho e^{-\phi t}.$$

As noted above, we assume that immediately after tagging, we expect a proportion $(1-\rho)$ of the fish to lose their tags. Additionally, we assume that a proportion, q, of the fish die immediately from tagging. If the tagging took place in the late fall, recoveries may take place before the next year. We also assume that natural mortality occurs continuously throughout the year, but that fishing occurs only at one time at midyear.

To account for these losses prior to the first fishing season, we need to adjust N. The number of fish that are alive and retain their tags at the beginning of the first fishing season after tagging is

$$\left(N(1-q)\rho - \frac{r_0}{\lambda}\right)e^{-(M+\phi)t_F}$$

where r_0 is the number of tagged fish recovered during the late fall immediately after tagging, t_F is the fraction of year between the tagging and the next June, and M is the natural mortality, which is assumed constant for all years. Recall that v represents the proportion of fish that die naturally each year or lose their tags, i.e., $v = 1 - e^{-(M+\phi)}$. Note that our definition of v differs from Ricker's (1975) notation because his v included only natural mortality. If the reporting rate is λ, then at most

$$N^* = \left(N(1-q)\rho - \frac{r_0}{\lambda}\right)(1-v)^{t_F}\lambda$$

tags will subsequently be returned. We refer to N^* as the *effective number of fish released* because it corresponds to the number released just before the fishing season in an idealized experiment where there is no initial tagging mortality, no initial tag shedding, no natural mortality or shedding between the time of tagging and the first fishing season, and all tags are reported. Letting $\theta = (1-q)\rho\lambda$, we can write

$$N^* = (N\theta - r_0)(1-v)^{t_F}.$$

Note that $1-\theta$ represents the proportion of tags that disappear immediately from our view, i.e., the Type I losses identified by Beverton and Holt (1957).

The Type II losses identified by Beverton and Holt (1957) are natural mortality, fishing mortality, and tag loss. If natural mortality and fishing mortality are constant, then the proportion of fish (after adjusting for initial losses) that survive and retain their tags at the beginning of the yth fishing season is

$$[(1-u)(1-v)]^{y-1}.$$

During the yth fishing season, a proportion u of these fish will be caught and reported. Therefore, the expected number of tags returned in year y is

$$E(R_y) = N^*[(1-u)(1-v)]^{y-1}u.$$

A model for sequential fishing

Suppose fishing takes place each year in two nonoverlapping stages ($s = 1, 2$) with exploitation rates u_1 and u_2. Then the proportion of fish (after adjusting for initial losses) that will survive and retain their tags at the beginning of the first stage of the yth fishing season is

$$[(1-u_1)(1-u_2)(1-v)]^{y-1}.$$

Similarly, at the beginning of the second stage of the yth fishing season, the proportion is

$$[(1-u_1)(1-u_2)(1-v)]^{y-1}(1-u_1).$$

A model that varies with tag type and fishing gear

Our model is based on the sequential fishing model described above. The two stages of fishing we consider are the offshore fishery ($s = 1$), which occurs first, and the inshore fishery ($s = 2$), which occurs after the offshore fishery. The number of fish tagged is adjusted as described above, i.e., the number of fish tagged, N, is adjusted to N^*, the effective number of released fish at the start of the first fishing season after tagging. Returned tags are classified as coming from the inshore or offshore fishery based on the fishing gear type used.

Additionally, we classify tags by tag type, k. We assume that all tags are released simultaneously. Suppose that N_k tags of type k were released and that, for fall experiments, r_{s0k} of these were returned from stage s prior to the end of the year of tagging. Let the instantaneous shedding rate for tag type k be ϕ_k. Let θ depend on both tag type and on the fishery (inshore or offshore), i.e., for fishery s and tag type k, let $\theta = \theta_{sk}$.

The expected returns of tag type k from the offshore fishery in year y is

$$E(R_{1yk}) = N^*_{1k}[(1-u_1)(1-u_2)(1-v_k)]^{y-1}u_1$$

and from the inshore fishery is

$$E(R_{2yk}) = N^*_{2k}[(1-u_1)(1-u_2)(1-v_k)]^{y-1}(1-u_1)u_2$$

where $v_k = 1 - e^{-(M+\phi_k)}$ and $N^*_{sk} = (N_k\theta_{sk} - r_{s0k})e^{-(M+\phi_k)t_F}$.

In the above analysis, we again assume that the fishing mortality occurs during a short period of time each year. This

© 1997 NRC Canada

assumption is known as "Pope's approximation" in models of commercial catch-at-age data and is an excellent approximation to the Newfoundland cod data (Mertz and Myers 1996).

Unfortunately, we generally cannot simultaneously estimate all of the θ_{sk} parameters and the exploitation rates. To circumvent this problem, we assume that the effects of tag type, k, and fishing stage, s, enter into θ_{sk} multiplicatively. This allows us to consider separately the effects of tag type and fishing stage. To study the effects of tag type, an analysis of relative tag shedding, using the methods of Barrowman and Myers (1996), gave estimates of θ_{sk} relative to a reference tag type, $k = 1$, for each tag type, k, averaged over both fishing stages. For example, for the 1950's data, we let the external plastic tags be the reference type. Significant differences were found only between the internal and external tags used in the 1950's experiments. The θ for external tags was found to be 1.49 (SE = 0.09) times that for internal tags, and the ϕ for external tags was found to be 0.09 (SE = 0.02) greater than that for internal tags.

We can obtain information on the ratio of θ inshore to offshore from several sources. Assuming that the mortality associated with tagging and initial tag shedding is the same inshore and offshore, this is equivalent to examining the ratio of reporting rates inshore and offshore. There is reason to believe that the offshore reporting rate is quite low. In an experiment on English trawlers in which tags were secretly placed on cod caught at sea, Margetts (1963) found that only one third of the tags were subsequently reported by the fishermen. Horsted (1963) estimated the relative reporting rates of inshore Greenland fishermen and Portuguese dory-vessels, both have high reporting rates, to reporting rates of trawlers off Greenland. By examining the ratio of reported tags to landings for various groups, he found an average ratio of 3.37 for that region. He suggested that a minimum ratio of 2.5 should be used for trawlers. We also examined one tagging experiment carried out on the southeast shoal of the Grand Banks in 1955 that had no inshore returns. We were thus able to estimate θ and the mortality rate from this experiment. For trawlers, θ was estimated to be 0.175 (SE = 0.0977), which is approximately one quarter the θ estimated for the inshore for that period. We will initially consider an offshore θ fixed at one third of the inshore θ and examine the robustness of our conclusions to that assumption.

With these assumptions about the effects of tag type and fishing stage on θ_{sk} (Table 3), we need estimate just three parameters: θ_{21} (reporting rate × probability of initial tag retention × probability fish survive tagging for reference tag type inshore), u_1 (finite exploitation rate offshore), and u_2 (finite exploitation rate inshore).

The observed tag returns are modelled as independent Poisson random variables with expectations having the above form (Cormack and Skalski 1992; Green and Macdonald 1987). Extra-Poisson variability (overdispersion) is likely (Cormack and Skalski 1992) with the result that we may slightly underestimate the standard errors of our estimates. The log likelihood for our model is

$$\ell = \sum_{s=1}^{2}\sum_{k=1}^{K}\sum_{y=1}^{Y} r_{syk}\log E(R_{syk}) - E(R_{syk}) - \log r_{syk}!$$

Table 3. Base case settings.

	Parameters	
Tag type	Inshore θ	ϕ
External plastic	θ_{21}	0.09
Internal	$0.67\theta_{21}$	0
Disc	θ_{21}	0.02

Note: For the base case, $M = 0.2$, the first 5 yrs of tag return data are used, and we set the ratio of θ offshore to inshore = 1/3. The settings for inshore θ and for ϕ are given. θ_{21} is the parameter directly estimated in the model.

where r_{syk} is the observed number of tags of type k returned from fishing stage s, in year y, K is the total number of different tag types, and Y is the total number of years of tag returns used. Maximum likelihood estimation is then straightforward. We maximize the log likelihood using the BFGS positive definite secant update algorithm (Dennis and Schnabel 1983). Asymptotic standard errors and correlations of the estimates are calculated from the inverse of the Hessian matrix evaluated at the maximum (Cox and Hinkley 1974).

Data

During late spring and early summer, there is an inshore migration of cod that winter on the edge of the banks (Templeman 1974, 1977). Since we are interested in the exploitation rate of inshore populations, we will restrict our attention to tagging done close to shore outside of the summer months. All tagging studies were carried out by the Canadian Department of Fisheries and Oceans, Northwest Atlantic Fisheries Centre, St. John's, Nfld., or its predecessors, the Fisheries Research Board of Canada and the Newfoundland Fisheries Research Commission. Each tagging experiment will be identified by a number which consists of the last two digits of the year of release and a two digit sequential identifier. This will allow the raw data to be identified by other researchers.

The first data we use are from taggings carried out near St. John's in 1948, using internal tags made of 51 × 9.5 mm flat celluloid plastic placed within the body cavity (Table 4). We used published returns for this tagging that were not separated by gear type or by geographical region (Templeman and Fleming 1962). We will assume that the returns from this tagging were primarily inshore because the large increase in offshore fishing had not occurred by the time of the recoveries and only four of the recoveries were from offshore (Templeman and Fleming 1962). We had access to the information on the individual returns for all other data. There were also fish tagged using aluminum disk "bachelor-buttons" through the preopercular bone; however, these tags caused such a high mortality that we could not use them for making estimates of exploitation rate (Templeman and Fleming 1962).

In 1954, there were two inshore tagging experiments (Templeman 1963, 1974). About half of the tags were internal tags, as described above, of four different lengths: 51, 76, 102, and 127 mm. We combine the results for these tags because they were put on with equal frequency. External tags

© 1997 NRC Canada

Table 4. Tag releases and returns (years refer to years in which fish were recaptured during the same year as tagging, yr0, up to the sixth year posttagging, yr6).

Expr.	Year	Month	Day	Area	Tag	Released	Shore	yr0	yr1	yr2	yr3	yr4	yr5	yr6
4802	1948	10	20	3Lj	Internal	286	In	15	29	12	4	5	1	1
5406	1954	10	15	3Lq	Internal	400	Off	1	5	6	3	0	1	0
							In	2	35	19	7	2	6	1
					External plastic	482	Off	4	17	12	10	1	1	0
							In	0	62	31	12	4	2	0
5408	1954	11	10	3Lj	Internal	792	Off	1	18	11	4	1	0	0
							In	0	78	28	25	6	2	2
					External plastic	965	Off	0	32	27	12	5	3	3
							In	2	101	63	31	14	12	2
6208	1962	10	11	3Lb	Disc	336	Off	0	12	16	12	3	0	0
							In	3	48	29	6	4	6	5
6210	1962	11	10	3Lc	Disc	1008	Off	0	33	36	19	7	5	6
							In	0	133	76	19	10	9	2
6315	1963	10	6	3Lj	Disc	1008	Off	0	68	18	12	7	4	0
							In	49	297	59	25	11	4	2
6316	1963	10	18	3Lj	Disc	1008	Off	0	89	34	7	4	4	1
							In	27	232	63	33	9	5	4
6317	1963	10	25	3Ki	Disc	1008	Off	0	39	28	9	3	2	2
							In	0	224	70	62	35	9	20
6318	1963	11	11	3Kd	Disc	1008	Off	0	59	30	11	2	2	1
							In	3	112	49	40	15	15	8
6319	1963	11	6	3Lq	Disc	1008	Off	2	58	20	14	5	1	1
							In	9	240	82	48	13	8	4
6414	1964	10	18	3La	Disc	1008	Off	3	75	36	18	10	6	0
							In	13	142	39	38	10	12	3
6416	1964	11	20	3Lc	Disc	672	Off	0	50	24	17	10	4	1
							In	0	73	30	13	4	3	2
6505	1965	11	25	3Lj	Disc	1007	Off	0	67	45	17	7	6	1
							In	70	206	51	18	7	2	2
7905	1979	10	19	3Lf	Disc	193	Off	0	3	3	0	0	0	0
							In	2	32	7	1	0	0	1
					t-bar	163	Off	0	2	2	1	1	0	0
							In	1	19	10	4	2	3	0
8102	1981	3	14	3Ki	Disc	572	Off	0	4	5	2	2	1	2
							In	0	58	28	10	3	0	0
					t-bar	560	Off	0	3	4	8	1	7	1
							In	0	16	24	5	3	1	1
8405	1984	10	9	3Kd	Disc	129	Off	1	8	3	0	0	0	0
							In	0	7	1	1	1	1	0
					t-bar	130	Off	0	13	6	1	2	0	0
							In	1	5	2	0	0	0	0
9004	1990	3	24	3Lb	Disc	259	Off	0	0	1	—	—	—	—
							In	0	32	10	—	—	—	—
					t-bar	174	Off	0	0	1	—	—	—	—
							In	0	18	7	—	—	—	—
9101	1991	1	20	3Lb	t-bar	199	Off	0	0	—	—	—	—	—
							In	0	79	—	—	—	—	—

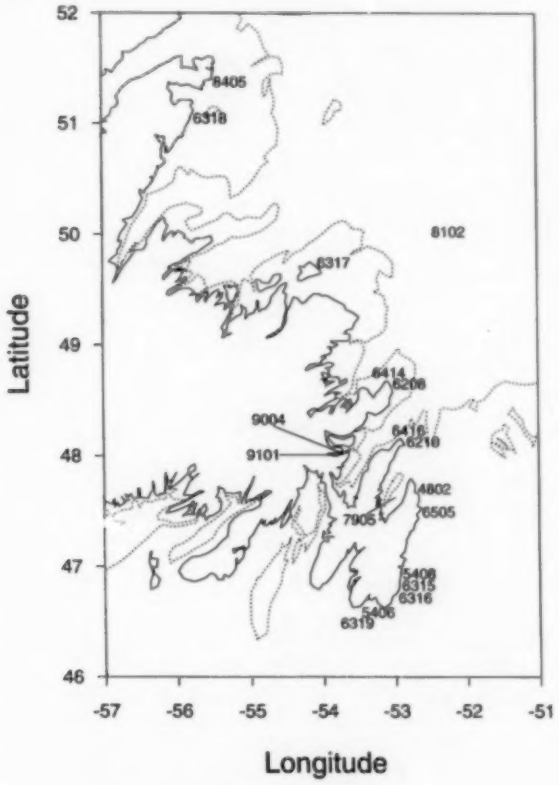
made of vinylite or celluloid with widths from 4.8 to 9.5 mm and with lengths from 20 mm to 76 mm were also used; these tags were attached by a variety of methods described in Templeman (1963). These different varieties were also put on in equal frequencies. We will consider only external tags attached to the dorsal fin because these appear to have had higher retention rates.

Between 1962 and 1965, tagging experiments were conducted using Petersen disk tags (Templeman 1977). Most of these tags were attached to the dorsal fins, but 12% were attached to the preopercular bone. We will analyze only the dorsal fin taggings. Some tags had "danglers" attached. These taggings were carried out by the same technicians using very similar methods throughout the study. These inshore tagging studies covered most of the region.

In the taggings after 1977, the tags were 2.5-cm Petersen

© 1997 NRC Canada

Fig. 1. Locations of inshore taggings examined. The tagging experiment is identified by a number that begins with the last two digits of the year of tagging (see Table 4). The broken line is the 200-m isobath.



disks attached through the posterior of the first dorsal fin, with or without a dangler (Lear 1984). Some fish were tagged using 1.5-cm spaghetti anchor t-bar tags attached through the base of the first dorsal, but we will not consider these results here to keep the models from becoming overly complicated. The results were similar when they were included.

We will limit our analysis to fish 50 cm or longer at the time of release. Cod were captured by baited hooks or trawls of short duration (Fig. 1); only fish in excellent condition were released. Each tagging episode typically took at least a week, so not all tags were placed on one group of fish.

We will consider two gear types: inshore gear comprising traps, baited hooks, jiggers, and gill nets, and offshore gear comprising trawlers. The reason for this breakdown is that reporting rates should be similar when fishermen handle fish individually. This division into gear types is a good approximation of fish caught close to shore and away from shore. There are exceptions to this rule, e.g., some gill nets are used in areas considerable distances from shore (Hutchings and Myers 1994), but such exceptions constitute only a very small fraction of the data (less than 2%). The inshore and offshore tag returns are compiled in Table 4. The offshore catch tended to precede the inshore catch (Fig. 2). This justifies our assumption that the offshore catch occurs first.

In our base case (Table 3), we will examine the 5 yr of recoveries from the beginning of the first new year after the tagging took place. We chose this time because the double tagging experiments could not be extrapolated beyond this (Barrowman and Myers 1996), and tag loss could have changed subsequently. Furthermore, it is unlikely that fishing mortality would remain reasonably constant for more than 5 yr. We will test the robustness of our results by making estimates over 4 and 6 yr.

Results

For each tagging experiment in Table 4, we extracted the observed returns and fit a sequence of models to the data (Table 5). We will begin with a base assumption (Table 3) and test the robustness of the conclusions by varying these assumptions. With our base assumptions, we estimate relatively high rates of exploitation for all time periods.

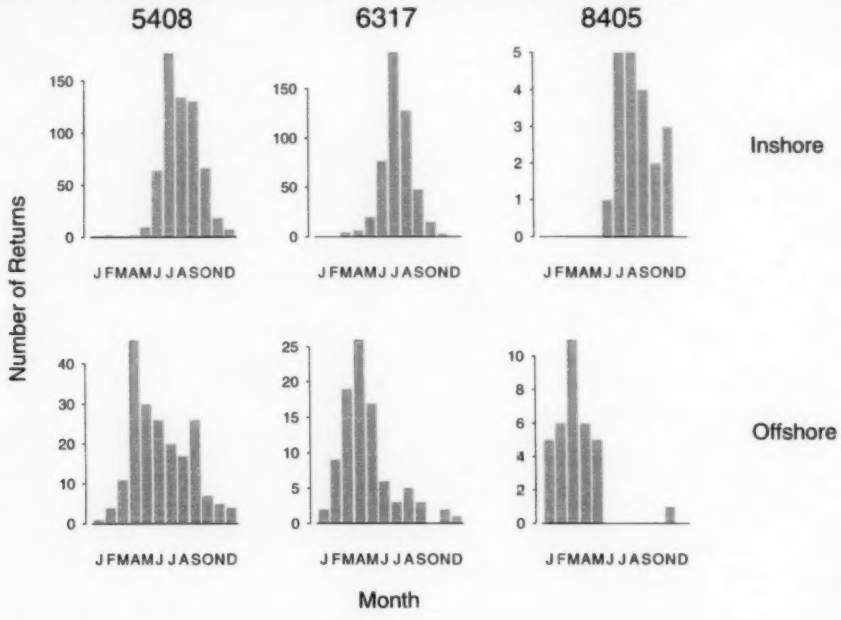
The proportion of tags that do not immediately disappear from view because of death caused by tagging, initial tag loss, and nonreporting, θ, is high in the 1950's and 1960's experiments, approximately 70% for externally tagged fish in the 1950's and over 75% in the 1960's. These high rates are a result of careful tagging and relatively high rewards for the tags. In the 1980's, the estimated inshore θ is much lower under our base assumption. Possibly, tag loss was higher during that period. Estimates of the inshore reporting rates obtained from interviews with fishermen were approximately 72% (Lear and Rice 1987), much lower than would be compatible with our estimates here. We suspect that the offshore reporting rate is much less than we have used in the base case; the estimates that assume that the ratio of the θ's was 0.2 were more reasonable, i.e., the estimate of the θ_0 is between 0.25 and 0.76.

In 1990 and 1991, there were inshore taggings in Trinity Bay in January or March (experiments 9004 and 9101). We use only 2 yr of recoveries for the 1990 release and one for the 1991 because of the cod fishing moratorium in 1992. The recovery rate of the 1990 experiment was much lower than for 1991 (Table 4). For the 1991 tagging experiment, there was only 1 yr of recovery, so we cannot use our model; nevertheless, some estimates are possible. Of the 476 cod larger than 50 cm tagged in Trinity Bay with Petersen disk tags in January, 212 tags were recovered in Trinity Bay and surrounding bays during the summer of 1991. Independent experiments show that approximately 13% of tagged cod die immediately from tagging during this period and that inshore reporting rate of tags is approximately 72% (Lear and Rice 1987). If the instantaneous natural mortality is 0.2, then approximately 294 fish were actually caught of the approximately 375 alive in the summer of 1991. This represents an exploitation rate of 78%, or an instantaneous fishing mortality of $1.54 \cdot yr^{-1}$ (shown on Fig. 3).

Our results on fishing mortality must be interpreted in light of probable stock structure mentioned in the introduction. Three of the taggings (experiments 7905, 9004, and 9101) were carried out deep inside bays and probably represent primarily bay stocks. Most of the rest of the taggings probably represent a combination of headland, bay, and offshore migrants. The fishing mortality estimated from these experiments should be viewed as that experienced by such

© 1997 NRC Canada

Fig. 2. Seasonal cycles of the inshore and offshore returns for three representative experiments.



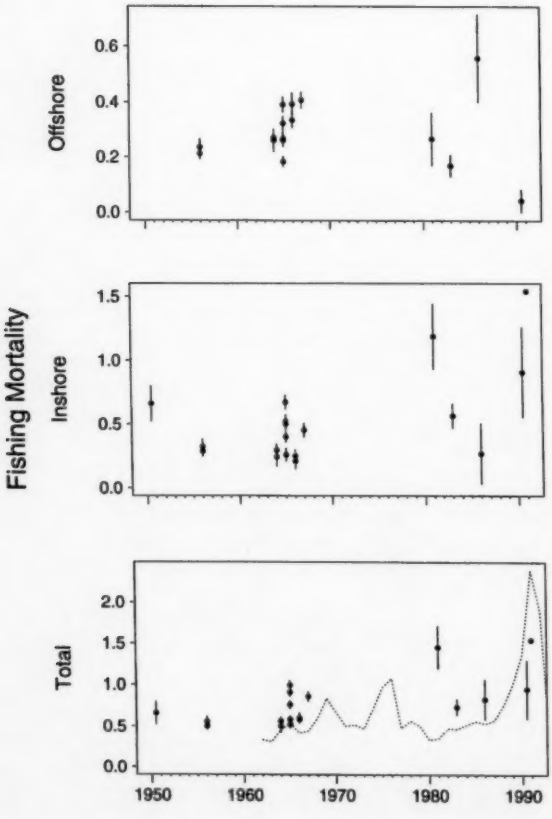


Fig. 3. Inshore, offshore, and total estimated mortality, with standard errors, from each tagging versus the midpoint of the period used to estimate mortality for the $M = 0.1$ case listed in Table 5, i.e., same as the base case (Table 3) except $M = 0.1$. There is no standard error for the 1991 estimate because only 1-yr returns were used in the estimate. The broken line on the bottom panel is the fully recruited fishing mortality estimated from the sequential population analysis for the whole population.

a mixture of fish. One of our taggings (experiment 8405) probably consisted almost entirely of offshore migrants; this group of fish had relatively low inshore fishing mortality and the highest offshore fishing mortality of any group of fish tagged. In contrast, experiment 8102 was not tagged close to shore (Fig. 1), and yet this group of fish was almost entirely exploited by the inshore fishery.

Robustness and violations of model assumptions

We will examine the robustness of our estimates to violations of model assumptions (reviewed by Pollock et al. 1991).

(1) Natural mortality is 0.2. The results of our robustness analysis show very small changes in the estimates of the fishing mortality over the range of assumptions we tested (Table 5). Using the alternative assumption that natural mortality is 0.1, we estimate a higher fishing mortality by about 10%. This usually resulted in a lower θ in the 1960's, which appears to be more reasonable because it is extremely unlikely that θ could be close to 1. For this to occur the product

© 1997 NRC Canada

Table 5. Parameter estimates × 100 (with standard errors) under various conditions.

Condition	Paramter	Experiment						
		4802	5406	5408	6208	6210	6315	6316
Base case	θ_{21}	31 (4.2)	80 (7.5)	83 (6)	100 (—)	85 (6.5)	98 (5)	100 (—)
	F_1		20 (2.9)	17 (1.9)	22 (3.7)	23 (2.6)	30 (2.5)	36 (2.7)
	F_2		26 (4.2)	23 (2.8)	22 (3.3)	24 (3.2)	59 (4.8)	46 (3.6)
	F_{total}	56 (14)	46 (6.2)	40 (4.2)	44 (6)	46 (5)	89 (5.6)	82 (5.2)
$m = 0.1$	θ_{21}	27 (3.2)	64 (5.2)	65 (3.9)	88 (9.7)	69 (4.6)	86 (4.3)	89 (4.7)
	F_1		23 (3)	21 (2)	26 (4.2)	27 (2.6)	32 (2.7)	39 (2.8)
	F_2		32 (4.5)	29 (3)	24 (4.8)	29 (3.4)	67 (5)	52 (4.3)
	F_{total}	66 (14)	56 (6.1)	50 (4.2)	50 (7.7)	56 (5)	99 (5.6)	91 (5.4)
4 yr	θ_{21}	32 (5)	76 (7.5)	83 (7.1)	100 (—)	82 (6.8)	95 (4.9)	100 (5.5)
	F_1		22 (3.4)	17 (2.2)	24 (4.3)	24 (2.9)	31 (2.7)	37 (2.9)
	F_2		29 (5.1)	22 (3.3)	22 (3.5)	25 (3.8)	64 (5.4)	49 (4.7)
	F_{total}	53 (16)	51 (7.5)	40 (5.1)	47 (6.8)	49 (6.1)	95 (6.3)	86 (6.2)
6 yr	θ_{21}	32 (4.2)	77 (6.6)	82 (5.4)	100 (—)	88 (6.4)	98 (5)	100 (—)
	F_1		21 (2.8)	18 (1.8)	20 (3.2)	23 (2.4)	30 (2.5)	34 (2.5)
	F_2		28 (4.1)	23 (2.6)	21 (3)	22 (2.8)	59 (4.6)	44 (3.4)
	F_{total}	54 (12)	49 (5.7)	41 (3.8)	41 (5.3)	45 (4.4)	89 (5.3)	78 (4.8)
Disc $\phi = 0.1$, internal $\phi = 0.1$	θ_{21}	37 (6.3)	100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	100 (—)
	F_1		16 (2.4)	15 (1.5)	21 (3.5)	20 (2.2)	27 (2.3)	32 (2.6)
	F_2		21 (2.3)	19 (1.4)	23 (3.3)	20 (1.9)	57 (4.1)	45 (3.5)
	F_{total}	46 (14)	37 (4)	34 (2.5)	44 (5.6)	40 (3.6)	85 (5.3)	78 (5)
Ratio of θ offshore to inshore = 0.2	θ_{21}		100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	100 (—)
	F_1		26 (3.4)	23 (2.2)	28 (4.1)	29 (2.9)	36 (2.7)	42 (2.8)
	F_2		22 (2.5)	20 (1.6)	23 (3.3)	21 (2)	57 (4.1)	46 (3.5)
	F_{total}		48 (5.2)	43 (3.4)	51 (6.4)	51 (4.3)	94 (5.4)	87 (5.2)
Ratio of θ offshore to inshore = 0.5	θ_{21}		67 (5.9)	69 (4.8)	91 (11)	70 (5)	84 (3.9)	84 (4.2)
	F_1		15 (2.4)	14 (1.6)	17 (3.4)	18 (2.1)	23 (2.1)	28 (2.3)
	F_2		30 (4.7)	26 (3.1)	23 (5.1)	28 (3.6)	67 (5)	53 (4.4)
	F_{total}		46 (6.2)	40 (4.2)	40 (7.7)	46 (5)	89 (5.6)	81 (5.4)

Note: In cases where parameter constraints were applied, standard errors could not be computed and are represented as (—). The parameter θ_{21} is the product of initial survival after tagging, initial tag retention, and reporting rate for the reference tag type in the inshore fishery. The parameters F_1 and F_2 are the offshore and inshore fishing mortalities, respectively (derived from the exploitation rates u_1 and u_2 estimated in the model). The estimate of total fishing mortality, $F_{total} = F_1 + F_2$, is also given. The first set of estimates represents the base case (Table 3), while the other sets of estimates are deviations from the base case.

of initial survival probability after tagging, tag retention, and reporting probability would have to be 1, which is unlikely.

(2) Mortality and reporting rates are constant over the estimation period. Fishing mortality increased in the late 1980's and early 1990's (Myers and Cadigan 1995*a*, 1995*b*). An increase in fishing mortality over time would tend to negatively bias the estimated fishing mortality because as fishing mortality increases over time, the rate of return of tagged fish stays high (suggestive of low mortality) for a while due to increasing catch rate of tagged fish. Thus, we may underestimate fishing mortality during this period. Other changes in mortality and reporting rates are likely to be smaller and may increase or decrease any one estimate, but should not systematically bias our results.

(3) The tag shedding rate is known. If the tag shedding rate was increased from 0.02 to 0.1 for the Petersen tags, then the estimated exploitation rate was usually decreased by less than 10%. Note that this tag shedding rate is clearly too high for the 1960's data because three of the θ's are estimated to be greater than 1, which is impossible.

(4) Mortality rates are not influenced by tagging. Experiments on mortality of tagged fish obtained from trawls and held for 2 wk indicate that mortality under these conditions is less than 13% (Lear and Rice 1987). These estimates are probably positively biased because some of the fish died when their tags snagged in the nets covering the tank. Furthermore, mortality associated with trawling fish from around 200 m is probably greater than that for fish obtained in shallower water. In any case, our estimates indicate that natural mortality plus tag-induced mortality could not be much

© 1997 NRC Canada

Table 5 (*concluded*).

Experiment									
6317	6318	6319	6414	6416	6505	7905	8102	8405	9004
100 (6.3)	88 (7.1)	96 (5.4)	100 (—)	99 (8.8)	97 (5.5)	38 (6.3)	32 (3.8)	49 (12)	24 (5.6)
16 (1.7)	22 (2.6)	23 (2.2)	29 (2.6)	33 (4.1)	37 (2.9)	26 (9.3)	15 (3.7)	50 (16)	3.9 (3.9)
33 (3.4)	20 (3)	43 (3.9)	22 (2)	17 (2.9)	39 (3.9)	110 (25)	48 (8.6)	23 (11)	81 (34)
48 (4.3)	43 (5)	66 (4.8)	51 (4.1)	50 (6.3)	76 (5.5)	130 (26)	63 (9.8)	73 (24)	85 (35)
81 (4.5)	70 (4.8)	82 (4.4)	86 (5.3)	82 (6.5)	85 (4.6)	34 (5.6)	28 (3.1)	42 (10)	22 (4.5)
18 (1.9)	27 (2.7)	26 (2.3)	33 (2.8)	39 (4.1)	41 (3)	26 (9.6)	17 (4)	56 (16)	4.2 (4.2)
40 (3.5)	26 (3.2)	50 (4)	25 (2.8)	21 (3.2)	45 (4.2)	120 (25)	56 (8.9)	27 (12)	91 (34)
58 (4.3)	53 (5)	76 (4.8)	58 (4.8)	60 (6.3)	86 (5.5)	140 (26)	73 (9.7)	83 (24)	95 (35)
100 (—)	83 (7.2)	96 (5.6)	100 (7.2)	98 (9.7)	95 (5.4)	38 (6.3)	33 (4.2)	46 (11)	24 (5.6)
15 (1.8)	25 (3.2)	23 (2.3)	32 (3.3)	33 (4.8)	38 (3.1)	25 (9.3)	13 (3.6)	63 (20)	3.9 (3.9)
32 (2.5)	23 (3.6)	43 (4.3)	23 (3.2)	17 (3.4)	42 (4.5)	110 (25)	45 (9.4)	29 (15)	81 (34)
47 (3.7)	48 (6.2)	66 (5.5)	55 (5.9)	51 (7.5)	80 (6.3)	130 (26)	58 (11)	92 (30)	85 (35)
100 (—)	89 (6.8)	97 (5.3)	100 (—)	98 (8.3)	98 (5.4)	40 (6.5)	34 (3.9)	49 (12)	24 (5.6)
13 (1.4)	21 (2.3)	23 (2.1)	30 (2.6)	33 (3.8)	37 (2.8)	22 (8.1)	16 (3.6)	51 (15)	3.9 (3.9)
30 (2.2)	20 (2.6)	42 (3.6)	22 (2)	17 (2.7)	38 (3.7)	88 (20)	44 (7.6)	24 (11)	81 (34)
43 (3)	41 (4.3)	65 (4.4)	52 (3.9)	50 (5.7)	75 (5.2)	110 (21)	60 (8.7)	75 (23)	85 (35)
100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	41 (6.9)	37 (4.6)	56 (15)	26 (7)
14 (1.6)	20 (2.2)	21 (2)	27 (2.4)	31 (3.5)	34 (2.8)	25 (9.1)	14 (3.5)	45 (16)	3.6 (3.7)
33 (2.4)	18 (1.7)	41 (3.1)	22 (2)	17 (2.1)	37 (3.2)	100 (25)	42 (8.4)	20 (11)	73 (35)
47 (3.3)	38 (3.4)	62 (4.2)	50 (3.8)	49 (4.9)	71 (5)	130 (26)	55 (9.8)	65 (24)	77 (36)
100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	45 (8.9)	39 (5.2)	74 (19)	25 (6.2)
20 (2)	29 (2.9)	29 (2.4)	36 (2.8)	42 (4.1)	44 (3.1)	38 (12)	22 (4.8)	57 (18)	6.3 (6.1)
34 (2.5)	19 (1.9)	42 (3.1)	23 (2)	18 (2.2)	38 (3.2)	97 (25)	42 (8.2)	16 (8.4)	79 (34)
54 (3.7)	48 (4.1)	71 (4.5)	59 (4.2)	60 (5.5)	82 (5.2)	130 (26)	63 (9.8)	73 (24)	85 (35)
87 (5.1)	71 (5.4)	82 (4.2)	84 (5.5)	75 (6.4)	79 (4.1)	34 (5.2)	29 (3.2)	37 (8.6)	23 (5.4)
12 (1.4)	18 (2.2)	18 (1.7)	23 (2.4)	29 (3.6)	29 (2.5)	18 (7.1)	11 (2.9)	43 (14)	2.6 (2.7)
37 (3.6)	25 (3.4)	49 (4.1)	25 (3.1)	22 (3.5)	47 (4.3)	120 (25)	52 (8.9)	30 (14)	82 (35)
48 (4.3)	43 (5)	66 (4.8)	48 (4.8)	50 (6.3)	76 (5.5)	130 (26)	63 (9.8)	73 (24)	85 (35)

greater than 0.1. It is possible that fish tagged with Petersen disks have a higher probability of becoming entangled in gill nets, and thus suffering higher fishing mortality. We do not believe that this is an important problem because gill nets deliver a relatively small proportion of the returns (approximately 10%), and similar estimates of fishing mortality were obtained when we examined the fishing mortality from tags that are not likely to increase catchability (internal tags or t-bar tags).

(5) The ratio of θ *inshore and offshore is known.* If the ratio of θ offshore to inshore is changed, then the largest change occurs in the ratio of inshore to offshore mortality; there is relatively little change in the overall exploitation rate. If the ratio is reduced to 0.2, then the estimated offshore mortality generally increases; however, this results in a θ greater than 1 for the 1960's. A more moderate reduction produces reasonable results.

(6) The year of the tag recovery is correctly tabulated. Some tags may be reported from fish caught in previous years. This type of misreporting is probably small, since we only used tags in which the location and gear type of the tag were also reported, and there were followup telephone interviews of any suspicious tags. Any such tabulation errors will result in a negative bias in the estimated exploitation rate (Pollock et al. 1991).

(7) The fate of each tagged fish is independent of the fate of other tagged fish. Violations of this assumption will not bias the estimates but will result in standard errors being underestimated (Pollock et al. 1991).

(8) All tagged fish have the same annual mortality and recovery probabilities. Heterogeneity of survival and recovery rates is almost certain to occur for a variety of reasons, e.g., tagged fish may be from more than one subpopulation. Nichols et al. (1982) and Pollock and Raveling (1982) found, using simulations, that if recovery rates were heterogeneous, e.g., we combined more than one type of tag type in the 1950's and 1960's, then no biases resulted. They also found that if mortality rates varied, e.g., different fishing mortalities among a group of tagged fish, the estimated fishing mortalities and exploitation rates would be positively biased. They

© 1997 NRC Canada

also found that this bias should be reduced if the recovery period is long, e.g., several years, and mortality is low. Given the relatively high mortality, long recovery period, and the fact that relatively discrete groups of tagged cod are examined, this positive bias should be small.

It is possible to compare our estimates of fishing mortality with those obtained from sequential population analysis (SPA; Fig 3). In these comparisons, we assumed that natural mortality was 0.1 instead of the usual 0.2. A lower natural mortality than the usual assumption of 0.2 for such a slow-growing northern population is consistent with estimates of natural mortality derived form evolutionary models (Myers and Doyle 1983).

The fishing mortality we estimate from the inshore tagging is generally higher than that estimated by SPA (Bishop et al. 1994; Myers and Cadigan 1995*a*, 1995*b*). This remains true if we use an estimate of 0.2 for natural mortality (Table 5). There are two reasonable explanations for the higher inshore fishing mortality. First, the exploitation rate for fish that remain inshore for most or all of the year could be much higher than that of offshore components, some of which may not migrate inshore at all. Second, the fishing mortality estimated from the SPA will be much less if there has been underreporting of commercial catches. We believe that both factors are important. Myers et al. (1996*a*) examined estimates of fishing morality from tagging data from mainly offshore stock components and found only that they gave higher estimates of fishing mortality than the SPA, but not as high as estimated here. Myers et al. (1997) tested fishing mortality estimated from SPA with those estimated directly from research surveys. Although they found evidence of large misreporting and discarding for young cod, the bias in the estimates of fishing mortality for older cod was present, but not large. Taken together, this evidence indicates a higher fishing mortality on inshore stock components than on offshore stock components.

The θ's for the 1980's and 1990's experiments were generally much lower. There are several reasons for this. First, there was much less hand processing of the fish during this period, i.e., fewer fish were hand split and salted. Second, the tag reward was much less than in previous years because the rewards had not kept up with inflation. Third, trawls were used during this period to obtain some of the fish for tagging, which may have resulted in a higher mortality associated with tagging.

Conclusion

Do inshore stocks exist?

Cod in the 2J3KL region have been managed on the assumption that they are a single stock. We believe that there is overwhelming evidence that inshore stock components exist. Based on tagging, morphometric, and meristic data, several researchers have concluded that northern cod comprise several substocks (e.g., Graham 1923; Thompson 1943; Templeman 1974, 1977). The existence of significant spatial and temporal variability in spawning location and spawning time, respectively, is consistent with the hypothesis that northern cod are not panmictic (Hutchings et al. 1993; Myers et al. 1993). Spatial variation in spawning location may be responsible for the spatial variability in recruitment documented in research surveys (Mertz and Myers 1994). Evidence of the existence of inshore stocks is further supported by evidence of inshore spawning locations (Neilsen 1895; Graham 1923; Hutchings et al. 1993; Wroblewski et al. 1994; Smedbol and Wroblewski 1997) and by recently documented differences in microsatellite DNA between cod overwintering in Trinity Bay and cod overwintering on the northern Grand Banks (Ruzzante et al. 1996).

Additional evidence of temporal differences in spawning time between inshore and offshore cod has been documented by studies of larval cod abundance in inshore waters. Methven and Bajdik (1994) indicated that 0-group cod collected inshore may originate from both offshore and coastal spawning populations. They observed two periods of high abundance of 0-group cod (August–September and October–November) at a single sampling site in southern Trinity bay and suggested that these cod may be progeny of (spatially or temporally) discrete inshore spawning events. In addition, Pinsent and Methven (1997), concluded that recently settled 0-group cod collected in coastal locations of southern Trinity Bay, Newfoundland, during autumn and early winter likely had a nearshore (Trinity Bay) origin based on spawning times calculated from otolith microstructure and local water temperatures.

Can an inshore fishery exert high fishing mortality?

Our analysis indicates that exploitation rates on inshore stock components of Atlantic cod have been very high at least since the late 1940's. Our high estimates of inshore fishing mortality are consistent with the hypothesis that inshore subpopulations of cod around Newfoundland have been greatly reduced or possibly eliminated. Quantitative analyses have clearly demonstrated that populations have very low probability of growing under such high levels of fishing mortality (Hutchings and Myers 1994).

We believe that the inshore fishery has effected very high mortality rates on these inshore subpopulations. This is evident in our estimates of inshore fishing mortality, but is also supported from other sources. The first tagging experiments in the Newfoundland region were carried out by Thompson (1943) in the 1930's. Although the type of tags used caused high mortality rates and had relatively low retention (Templeman and Fleming 1962) and, therefore, could not be used in our analysis, Thompson's results are consistent with a high fishing mortality rate on inshore subpopulations during the 1930's. Twelve percent of the fish tagged inshore were returned in the first year after tagging, and only 3.025% were returned later. Given the high tag-induced mortality, the low tag retention rate, and an unknown reporting rate, it seems likely that the exploitation rate must have been higher than 25% for 12% of the tags to be returned the first year.

Support for the hypothesis that inshore stock components have been overexploited can be seen in the drastic decline in catch per unit effort from inshore fixed gear, e.g., cod traps and gill nets. Hutchings and Myers (1995) showed that catch per cod trap declined from over 200 tonnes per trap to 50 tonnes per trap between 1938 and 1945 in Labrador. Templeman (1966) showed that catch per man declined for northern cod between 1956 and 1964; however, this decline was concurrent with an increase in fishing effort offshore by foreign trawlers and inshore by improved gill nets (Hutchings and Myers 1995).

© 1997 NRC Canada

Hutchings and Myers (1994) showed that catch per cod trap and catch per gill net declined between 1987 and 1991 in all inshore areas in the 2J3KL region. These declines in catch rates, derived from sociological data on purchase slips, have been confirmed from interviews and logbooks from individual fishers (J.A. Hutchings, unpublished data). The decline in the gillnet catch rates occurred first inshore and then further offshore. This pattern is consistent with the hypothesis that inshore subpopulations were reduced before subpopulations that migrated to a lesser extent inshore (Hutchings and Myers 1995).

Our analysis of the 1991 tagging in Trinity Bay bears on the causes of the recent collapse of the northern cod stock. It has been suggested that the collapse was caused by an increase in natural mortality in 1991 (discussed in Myers and Cadigan 1995*b*). Our analyses demonstrate that the fish from this stock component in 1991 did not suffer extraordinary natural mortality and that the fishing mortality on them was very high in 1991. We conclude from the results of Hutchings and Myers (1994), Myers and Cadigan (1995*b*), Hutchings (1996), and Myers et al. (1996*a*, 1996*b*, 1997) that the collapse of northern cod was caused by overfishing.

The population dynamics of overexploitation of a mixed fishery with one component more catchable than the other are well understood. The population that is more catchable will be overfished or eliminated entirely (Clark 1990). That is, the offshore components of the population will allow exploitation of the inshore components to continue even when the inshore components are reduced to a very low level. The challenge in fisheries management is to devise a management policy that can effectively protect inshore subpopulations from overexploitation. Until recently, this fishery has been managed with virtually no limits on inshore fishing effort; this policy should be changed in the future.

Future tagging experiments

In the past, monitoring the inshore subpopulations and fishing mortality has not been possible. The inshore region is difficult to sample using traditional trawl or acoustic surveys because of its rough bottom, deep canyons, and large area. The resumption of an inshore tagging program would allow estimates of inshore fishing mortality to be obtained. If tagging were carried out over several years in the same location, it would be possible to use Brownie models, which allow many of the model assumptions to be tested.

Clearly, tagging can give reliable estimates of fishing mortality on stock components. Several points need to be considered in future experiments. (1) Double tagging experiments should be carried out to estimate tag loss. (2) At most, two types of tags should be applied. (If more than two types are used, it is difficult to achieve sufficiently large sample sizes to make valid comparisons of tag types.) (3) A portion of the tagged fish should be kept for at least a week after tagging in an aquarium or field cage to determine immediate death due to tagging. (4) Methods for tagging should be kept as constant as possible using only trained, closely supervised crews; otherwise, there can be considerable variation in tag return rates among and within experiments. (5) Taggings should be repeated in the same region in more than one year to test model assumptions using methods similar to the Brownie models. (6) Tag rewards should be sufficiently high to assure high probability of a tag being returned. (7) Some high rewards for tags, to encourage near 100% reporting of tags if they are detected, should be used so that reporting rate for standard tags can be estimated (Henny and Burnham 1976). If these conditions are met, it should be possible to use mark–recapture methods such as the ones developed here to estimate exploitation rates.

Acknowledgements

John Pope and Henry Lear were the first to realize that these data showed very high fishing mortality by the inshore fishery; their insight was crucial for this project. The tagging data were collected by the gadoid section of the Department of Fisheries and Oceans, St. John's, under the direction of W. Templeman, H. Lear, and C. Bishop. This work was supported by the Northern Cod Science Program. We thank P. Penney and C. Taggart for assistance in organizing the data. Bruce Atkinson, John Hoenig, Henry Lear, George Lilly, and Carl Schwartz provided useful comments on the manuscript.

References

Barrowman, N.J., and Myers, R.A. 1996. Estimating tag shedding rates for experiments with multiple tag types. Biometrics, **52**: 228–234.

Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. 2. No. 19.

Bishop, C.A., Anderson, J., Dalley, E., Davis, M.B., Murphy, E.F., Rose, G.A., Stansbury, D.E., Taggart, C., and Winters, G. 1994. An assessment of the cod stock in NAFO divisions 2J+3KL. NAFO SCR Doc. 94/40.

Brownie, C., and Pollock, K.H. 1985. Analysis of multiple capture–recapture data using band-recovery methods. Biometrics, **41**: 411–420.

Clark, C.W. 1990. Mathematical bioeconomics. 2nd ed. Wiley-Interscience, New York.

Cormack, R.M., and Skalski, J.R. 1992. Analysis of coded wire tag returns from commercial catches. Can. J. Fish. Aquat. Sci. **49**: 1816–1825.

Cox, D.R., and Hinkley, D.V. 1974. Theoretical statistics. Chapman and Hall, London, U.K.

Dennis, J.E., and Schnabel, R.B. 1983. Numerical methods for unconstrained optimization and nonlinear equations. Prentice-Hall, Englewood Cliffs, N.J.

Graham, M. 1923. Observations on the natural history of Newfoundland shore cod. Annu. Rep. Mar. Fish., Newfoundland.

Green, P.E.J., and Macdonald, P.D.M. 1987. Analysis of mark–recapture data from hatchery-raised salmon using log-linear models. Can. J. Fish. Aquat. Sci. **44**: 316–326.

Henny, C.J., and Burnham, K.P. 1976. A reward band study of mallards to estimate band reporting rates. J. Wildl. Manage. **41**: 1–14.

Horsted, S.A. 1963. On non-reported recaptures from Danish tagging experiments on cod, Subarea 1. Int. Comm. Northwest Atl. Fish. Spec. Publ. **4**: 22–25.

Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock collapse. Can. J. Fish. Aquat. Sci. **53**: 943–962.

Hutchings, J.A., and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. **51**: 2126–2146.

Hutchings, J.A., and Myers, R.A. 1995. The biological collapse of Atlantic cod off Newfoundland and Labrador: an exploration of historical changes in exploitation, harvesting technology, and

© 1997 NRC Canada

management. *In* The North Atlantic fisheries: successes, failures and challenges. *Edited by* R. Arnason and L. Felt. Institute of Island Studies, University of Prince Edward Island, Charlottetown, P.E.I. pp. 37–93.

Hutchings, J.A., Myers, R.A., and Lilly, G.R. 1993. Geographic variation in the spawning of Atlantic cod, *Gadus morhua*, in the northwest Atlantic. Can. J. Fish. Aquat. Sci. **50**: 2457–2467.

Lear, W.H. 1984. Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, as inferred from tagging studies. J. Northwest Atl. Fish. Sci. **5**: 143–159.

Lear, W.H., and Rice, J.C. 1987. Proportions of Atlantic cod (*Gadus morhua*) of the 2J3KL stock components taken by the inshore fishery as estimated by offshore tagging. CAFSAC Res. Doc. 87/3.

Margetts, A.R. 1963. The measurement of the efficiency of recovery and reporting of tags from recaptured fish. Int. Comm. Northwest Atl. Fish. Spec. Publ. **4**: 255–257.

Mertz, G., and Myers, R.A. 1994. The ecological impact of the great salinity anomaly in the northern Northwest Atlantic. Fish. Oceanogr. **3**: 1–14.

Mertz, G., and Myers, R.A. 1996. An extended cohort analysis: incorporating the effect of seasonal catches. Can. J. Fish. Aquat. Sci. **53**: 159–163.

Methven, D.A., and Bajdik, C. 1994. Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 78–90.

Myers, R.A., and Cadigan, N.G. 1995*a*. Statistical models for catch at age data with correlated errors. Can. J. Fish. Aquat. Sci. **52**: 1265–1273.

Myers, R.A., and Cadigan, N.G. 1995*b*. Was an increase in natural mortality responsible for the collapse of northern cod? Can. J. Fish. Aquat. Sci. **52**: 1274–1285.

Myers, R.A., and Doyle, R.W. 1983. Predicting natural mortality rates and reproduction–mortality trade-offs from fish life history data. Can. J. Fish. Aquat. Sci. **40**: 612–620.

Myers, R.A., Mertz, G., and Bishop, C.A. 1993. Cod spawning in relation to physical and biological cycles of the northern Northwest Atlantic. Fish. Oceanogr. **3**: 154–165.

Myers, R.A., Barrowman, N.J., Hoenig, J.M., and Qu, Z. 1996*a*. The collapse of cod in Eastern Canada: the evidence from tagging data. ICES J. Mar. Sci. **53**: 629–640.

Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1996*b*. Hypotheses for the decline of cod in the North Atlantic. Mar. Ecol. Prog. Ser. **138**: 293–308.

Myers, R.A., Hutchings, J.A., and Barrowman, N.J. 1997. Why do fish stocks collapse. Ecol. Appl. (In press)

Neilsen, A. 1895. Operations at Dildo Island Marine Hatchery. *In* Annual report of the Newfoundland Department of Fisheries, for the year 1894. J.W. Withers, St. John's, Nfld. pp. 26–48.

Nichols, J.D., Stokes, S.L., Hines, J.E., and Conroy, M.J. 1982. Additional comments on the assumptions of homogeneous survival rates in modern bird banding estimation models. J. Wildl. Manage. **46**: 953–962.

Pinsent, D.L., and Methven, D.A. 1997. Protracted spawning of Atlantic cod (*Gadus morhua*) in Newfoundland waters: evidence from otolith microstructure. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Pollock, K.H. 1991. Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. J. Am. Stat. Assoc. **86**: 225–238.

Pollock, K.H., and Raveling, D.G. 1982. Assumptions of modern band-recovery models with emphasis on heterogeneous survival rates. J. Wildl. Manage. **46**: 88–98.

Pollock, K.H., Hoenig, J.M., and Jones, C.M. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. Am Fish. Soc. Symp. **12**: 423–434.

Ricker, W.E. 1958. Handbook of computations for biological statistics of fish populations. Bull. Fish Res. Board Can. No. 119

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Ruzzante, D.E., Taggart, C.T., Cook, D., and Goddard, S. 1996. Genetic differentiation between inshore and offshore Atlantic cod (*Gadus morhua*) off Newfoundland: microsatellite DNA variation and antifreeze level. Can. J. Fish. Aquat. Sci. **53**: 634–645.

Smedbol, R.K., and Wroblewski, J.S. 1997. Evidence for inshore spawning of northern Atlantic cod (*Gadus morhua*) in Trinity bay, Newfoundland, 1991–1993. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1). This issue.

Templeman, W. 1963. Comparison of returns from different tags and methods of attachment used in cod tagging in the Newfoundland area, 1954 and 1955. ICNAF Spec. Publ. **4**: 272–287.

Templeman, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Board Can. No. 154.

Templeman, W. 1974. Migrations and intermingling of Atlantic cod (*Gadus morhua*) stocks of the Newfoundland area. J. Fish. Res. Board Can. **31**: 1073–1092.

Templeman, W. 1977. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962–66. ICNAF Res. Bull. **14**: 5–50.

Templeman, W., and Fleming, A.M. 1962. Cod tagging in the Newfoundland area during 1947 and 1948. J. Fish. Res. Board. Can. **19**: 445–487.

Thompson, H. 1943. A biological and economic study of cod (*Gadus morhua*) in the Newfoundland area. Res. Bull. (Fish.) Nfld. Dep. Nat. Resour. No. 14.

Wroblewski, J.S., Bailey, W.L., and Howse, K.A. 1994. Observations of adult Atlantic cod (*Gadus morhua*) overwintering in nearshore waters of Trinity Bay, Newfoundland. Can. J. Fish. Aquat. Sci. **51**: 142–150.

© 1997 NRC Canada

National Research Council Canada

Conseil national de recherches Canada

NRC · CNRC

Research Journals

† Biochemistry and Cell Biology
• Canadian Journal of Botany
• Canadian Journal of Chemistry
• Canadian Journal of Earth Sciences
‡ Canadian Journal of Fisheries and Aquatic Sciences
† Canadian Journal of Forest Research
• Canadian Journal of Microbiology
† Canadian Journal of Physics
‡ Canadian Journal of Physiology and Pharmacology
• Canadian Journal of Zoology
† Canadian Journal of Civil Engineering
• Genome
† Canadian Geotechnical Journal
† Environmental Reviews

‡ **Electronic version available**
† **Electronic version available in 1997**

Subscription Office, M-55
NRC Research Press
National Research Council Canada
Ottawa, ON K1A 0R6
Canada
Tel.: 613-993-9084
Fax.: 613-952-7656
E-mail: research.journals@nrc.ca
URL: http://www.nrc.ca/cisti/journals/rj.html

Revues scientifiques

† Biochimie et biologie cellulaire
• Revue canadienne de botanique
• Revue canadienne de chimie
• Revue canadienne des sciences de la Terre
‡ Journal canadien des sciences halieutiques et aquatiques
† Revue canadienne de recherche forestière
• Revue canadienne de microbiologie
† Revue canadienne de physique
‡ Revue canadienne de physiologie et pharmacologie
• Revue canadienne de zoologie
† Revue canadienne de génie civil
• Génome
† Revue canadienne de géotechnique
† Dossiers environnement

‡ **Disponible en version électronique**
† **Disponible en version électronique en 1997**

Bureau d'abonnements, M-55
Presses scientifiques du CNRC
Conseil national de recherches du Canada
Ottawa, ON K1A 0R6
Canada
Tél. : 613-993-9084
Télécopieur : 613-952-7656
Courrier électronique : research.journals@nrc.ca
URL : http://www.nrc.ca/cisti/journals/rj.html

Contents (concluded) / Table des matières (suite et fin)

Y. Lambert and J.-D. Dutil	**104–112**	Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of Atlantic cod (*Gadus morhua*)?
M. Krohn, S. Reidy, and S. Kerr	**113–121**	Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*)
M.P.M. Burton, R.M. Penney, and S. Biddiscombe	**122–131**	Time course of gametogenesis in Northwest Atlantic cod (*Gadus morhua*)
D.B. Atkinson, G.A. Rose, E.F. Murphy, and C.A. Bishop	**132–138**	Distribution changes and abundance of northern cod (*Gadus morhua*), 1981–1993
W.G. Warren	**139–148**	Changes in the within-survey spatio-temporal structure of the northern cod (*Gadus morhua*) population, 1985–1992
E. Colbourne, B. deYoung, and G.A. Rose	**149–157**	Environmental analysis of Atlantic cod (*Gadus morhua*) migration in relation to the seasonal variations on the Northeast Newfoundland Shelf
J.T. Anderson and E.L. Dalley	**158–167**	Spawning and year-class strength of northern cod (*Gadus morhua*) as measured by pelagic juvenile cod surveys, 1991–1994
E.L. Dalley and J.T. Anderson	**168–176**	Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland
R.K. Smedbol and J.S. Wroblewski	**177–186**	Evidence for inshore spawning of northern Atlantic cod (*Gadus morhua*) in Trinity Bay, Newfoundland, 1991–1993
D.C. Schneider, E.L. Dalley, and D.A. Methven	**187–199**	Geographic contraction in juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances
E.G. Dawe, E.L. Dalley, and W.W. Lidster	**200–208**	Fish prey spectrum of short-finned squid (*Illex illecebrosus*) at Newfoundland
G.B. Stenson, R.A. Myers, I-H. Ni, and W.G. Warren	**209–216**	Pup production and population growth of hooded seals (*Cystophora cristata*) near Newfoundland, Canada
M.J. Morgan, E.M. DeBlois, and G.A. Rose	**217–223**	An observation on the reaction of Atlantic cod (*Gadus morhua*) in a spawning shoal to bottom trawling
R.A. Myers, N.J. Barrowman, and J.A. Hutchings	**224–235**	Inshore exploitation of Newfoundland Atlantic cod (*Gadus morhua*) since 1948 as estimated from mark–recapture data

National Research Council Canada
Ottawa, Canada K1A 0R6

Conseil national de recherches Canada
Ottawa, Canada K1A 0R6

Canadian Journal of Fisheries and Aquatic Sciences

Volume 54, Supplement 1, 1997

Journal canadien des sciences halieutiques et aquatiques

Volume 54, supplément 1, 1997

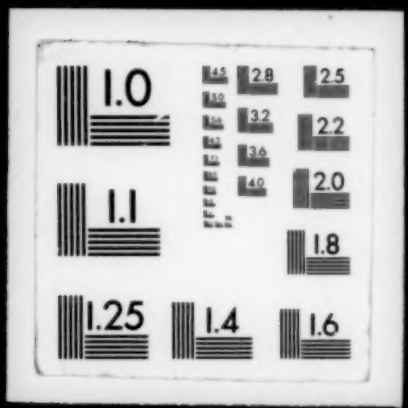
J.S. Campbell	**1**	Introduction to the Northwest Atlantic Cod Symposium
P. Pepin, D.C. Orr, and J.T. Anderson	**2–10**	Time to hatch and larval size in relation to temperature and egg size in Atlantic cod (*Gadus morhua*)
C.M. Herbinger, R.W. Doyle, C.T. Taggart, S.E. Lochmann, J.M. Wright, A.L. Brooker, and D. Cook	**11–18**	Family relationships and effective population size in a natural cohort of Atlantic cod (*Gadus morhua*) larvae
D.L. Pinsent and D.A. Methven	**19–24**	Protracted spawning of Atlantic cod (*Gadus morhua*) in Newfoundland waters: evidence from otolith microstructure
D.W. Ings, D.C. Schneider, and D.A. Methven	**25–29**	Detection of a recruitment signal in juvenile Atlantic cod (*Gadus morhua*) in coastal nursery areas
S.J. Prinsenberg, I.K. Peterson, S. Narayanan, and J.U. Umoh	**30–39**	Interaction between atmosphere, ice cover, and ocean off Labrador and Newfoundland from 1962 to 1992
J.W. Loder, G. Han, C.G. Hannah, D.A. Greenberg, and P.C. Smith	**40–56**	Hydrography and baroclinic circulation in the Scotian Shelf region: winter versus summer
D. Gilbert and B. Pettigrew	**57–67**	Interannual variability (1948–1994) of the CIL core temperature in the Gulf of St. Lawrence
E. Colbourne, B. deYoung, S. Narayanan, and J. Helbig	**68–80**	Comparison of hydrography and circulation on the Newfoundland Shelf during 1990–1993 with the long-term mean
J.W. Kiceniuk and E. Colbourne	**81–87**	Relating oxygen levels in the Newfoundland offshore waters to the physiology of Atlantic cod (*Gadus morhua*)
S.V. Goddard, M.J. Morgan, and G.L. Fletcher	**88–93**	Influence of plasma antifreeze glycoproteins on temperature selection by Atlantic cod (*Gadus morhua*) in a thermal gradient
G.L. Fletcher, J.S. Wroblewski, M.M. Hickey, B. Blanchard, M.H. Kao, and S.V. Goddard	**94–98**	Freezing resistance of caged Atlantic cod (*Gadus morhua*) during a Newfoundland winter
J.-D. Dutil, Y. Lambert, and E. Boucher	**99–103**	Does higher growth rate in Atlantic cod (*Gadus morhua*) at low salinity result from lower standard metabolic rate or increased protein digestibility?

Continued on inside back cover / Suite au verso

Canada

Typeset and printed in Canada by / Composé et imprimé au Canada par University of Toronto Press Inc.

0706-652X(1997)54+1;1-J


1.0
1.1
1.25
1.4
1.6
1.8
2.0
2.2
2.5
2.8
3.2
3.6
4.0
4.5
5.0